

BIOTIC COMMUNITIES OF THE NORTHERN DESERT SHRUB  
BIOME IN WESTERN UTAH

REED W. FAUTIN  
*University of Illinois*  
*Champaign, Illinois*

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## INTRODUCTION

### THE BIOTIC COMMUNITY CONCEPT

It has been only within the present century that the true significance of plant and animal community relationships has been recognized and the basic concepts of biotic communities developed. The recognition of plant communities and their distinctiveness came about as a natural consequence of the differences in the physiognomy of such communities, but the recognition of animal communities has been delayed on account of the motility and less conspicuous nature of the components. Sea-bottom animal communities were among the first to be described, probably because the animals concerned were less motile and formed a more conspicuous unit, the plants being the less conspicuous components in such situations.

The concept of the co-existence of plant and animal communities has been even slower in its development. The history of this concept is given by Clements & Shelford (1939), who were among the first to recognize the community relationships between plants and animals. Clements (1905) suggested that plant and animal communities frequently coincided. Vestal (1913) then pointed out that the relationships between plant and animal communities are so intimate that both may be considered as one biotic unit. At about the same time, Shelford (1913) emphasized the interactions between plants and animals and the importance of both components in the succession and development of biotic communities. Since then the intimate relationships between the plant and animal components of terrestrial biotic communities have been described by numerous students and co-workers of Shelford.

### ECOLOGICAL INVESTIGATIONS WITHIN UTAH AND VICINITY

Inasmuch as the science of bio-ecology has developed largely within the prairie and deciduous forest areas of the United States, the major investigations upon which it is based have been concerned with the biotic communities of those areas. Most investigators within the Great Basin Region have been concerned with the flora and fauna from a taxonomic and distributional point of view, and have used the life zones of Merriam (1898) as a basis for describing the distribution of the plant and animal components concerned. Most of the major bio-ecological studies have been concerned with the plant and animal communities of the mountains at elevations above 5,000 feet (Svihla 1932; Rasmussen 1941; Hayward 1945).

An investigation of the biotic communities of Zion Canyon in southern Utah by Woodbury (1933) was concerned primarily with the succession of the plant

components, although the invertebrate and vertebrate animals were included and their biotic relationships within the communities described.

The succession of plant communities occurring on the volcanic deposits in the Snake River plains area of southern Idaho has been investigated by Egger (1941), and the plant communities of southeastern Washington and adjacent Idaho have been very intensively studied by Weaver (1917) and Daubenmire (1942).

Hardy (1945) investigated the effects of various soil characteristics on the distribution of small mammals in the vicinity adjacent to St. George in southwestern Utah. The composition of various plant communities and their relationships to the distribution of certain mammals are described.

No attempt has been previously made to investigate the biotic communities of western Utah although detailed studies have been made of the plant communities and their relationships to soil conditions in Tooele Valley (Kearney, Briggs, Shantz, McLane, & Piemeisel 1914) and in Escalante Valley (Shantz & Piemeisel 1940). Some of the plant communities at the Desert Range Experiment Station in Pine Valley are described by Stewart & Keller (1936) in which they analyze statistically the correlation between various components in these communities. The effects of over-grazing on the plant communities of Pine Valley and Wah Wah Valley, with implications as to the trends in succession, are described by Stewart, Cottam, & Hutchings (1940).

In keeping with the general trend in the development of bio-ecology, the animal community relationships have been investigated far less than the plants. Taxonomic relations, geographic distribution and occasional life history studies have been of primary concern up to the present time. The work of Linsdale (1938), on the fauna of the Toyabe Mountains and adjacent valleys of central Nevada, includes observations on 215 species of vertebrates and their responses to certain environmental factors but no attempt is made to analyze them in terms of community relationships.

Since there had been no attempt to study and describe the biotic communities in western Utah this investigation was undertaken for that purpose. The field work involved was done during a part of two years, from June to September, 1939, and from April to September, 1940. Quantitative methods were employed in studying both the plant and animal components, supplemented by general observations and extensive cruising. An attempt was made to cover as much of the region outside the intensively studied areas as possible to obtain information concerning the general extensiveness, distribution, and

character of the various biotic communities. The communities investigated can hardly be considered as virgin because the activities of man, with the introduction of his domestic animals and his predator control practices, have undoubtedly altered the composition of the communities concerned and distorted the biotic relationships between some of the components. Consequently, the findings of the writer apply to the communities as they exist today. Certain general ecological relationships obtained from this investigation will apply to other similar communities within the same biome but the composition of communities in other areas may vary considerably on account of differences in physiography, soil composition, climatic variations, and the economic pursuits of man.

#### ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to Professor V. E. Shelford under whose direction this investigation was conducted. His suggestions, encouragement, and aid in placing necessary equipment at the writer's disposal have been invaluable. His assistance included a visit to the study areas during the summer of 1938 at which time the problem was outlined. Appreciation is also extended to the Society of Sigma Xi for awarding the writer a Grant-in-aid which was used in the completion of the problem in the summer of 1940. Dr. George Stewart and Mr. Selar Hutchings of the U. S. Forest Service provided the writer with living quarters at the Desert Range Experiment Station during a part of this investigation and also permitted the writer to use certain climatic data which had been recorded at the station.

Without the assistance of the many specialists who aided in the determination of the plants and animals collected, the identification of the numerous biotic components involved in this study would have been impossible. The cooperation of these people is greatly appreciated and the writer's gratitude is extended to the following: B. F. Harrison (plants); E. Raymond Hall and S. D. Durrant (mammals); Nathan Banks and H. E. Ewing (Acarina); R. V. Chamberlin and R. A. Cooley (Arachnida); Harlow B. Mills and G. Glance (Collembola); John W. E. Rehn (Orthoptera); J. C. Crawford (Thysanoptera); Herbert Ruckes, H. N. Knight, H. M. Harris, and H. G. Barber (Hemiptera); W. T. Davis, P. W. Oman, George F. Knowlton, P. N. Mason, and Harold Morrison (Homoptera); E. A. Chapin, H. S. Barber, R. E. Blackwelder, W. S. Fisher, L. L. Buchanan, and W. H. Anderson (Coleoptera); J. F. G. Clarke, and Carl Heinrich (Lepidoptera); C. T. Greene, Alan Stone and David G. Hall (Diptera); C. R. W. Muesebeck, A. B. Gahan, R. A. Cushman; M. R. Smith and Clarence E. Mickel (Hymenoptera).

#### THE REGION STUDIED

##### HISTORY AND EXTENT OF THE GREAT BASIN

When the early American explorers began to push westward beyond the Rocky Mountains they soon

became aware of the distinctiveness of the area which lay between the Wasatch range of the Rocky Mountains on the east and the Sierra Nevadas on the west. This vast area of approximately 210,000 square miles is unique in that there is no drainage system or systems which lead to the ocean. The geological history, physical features, and extent of this area have been described in detail by Russell (1883) and Gilbert (1890). It is a large basin containing numerous mountain ranges which run in a general north and south direction and which consequently divide the area into many smaller basins, each of which usually has its own drainage system terminating at the lowermost parts of the valley in a barren playa, a mud flat, or a lake.

Fremont (1845) who is given credit for giving this area its present name, the "Great Basin," describes it as follows in his journal of 1841 (p. 174):

"This mountainous region connects itself in the southward and westward with the elevated country belonging to the Cascade or California range; and, as will be remarked in the course of the narrative, forms the eastern limit of the fertile and timbered lands along the desert and mountainous region included within the Great Basin—a term which I apply to the immediate region between the Rocky Mountains and the West range, containing many lakes, with their own system of rivers and creeks, (of which the Great Salt is the principal), and which have no connection with the ocean, or the great rivers which flow into it. This Great Basin is yet to be adequately explored."

Within the Great Basin area of Utah there are a number of distinct independent drainage basins, the principal ones of which include the Escalante Desert, the Sevier Desert, Preuss Valley (now called Wah Wah Valley), White Valley, Snake Valley, Rush Valley, Cedar Valley, the upper portion of Pocatello Valley, the Pilot Peak Basin, and the Basin of the Great Salt Lake. These valleys and basins, together with a number in western Nevada, were at one time a part of two large Quaternary lakes. Lake Lahonton, situated at the base of the Sierra Nevada Mountains and fed by their snows, covered an area of 9,100 square miles. Lake Bonneville, situated on the eastern side of the Great Basin, was fed by snows from the Wasatch and Uinta Mountains and at the time of its maximum extent covered an area of 19,750 square miles. The evaporation of these large bodies of water and continual evaporation of the water which drains into these valleys and basins has resulted in the deposition of enormous quantities of mineral salts. So impregnated with salt are the bottoms of many basins, such as Psoob Valley in Nevada and the area adjacent to Great Salt Lake and Sevier Lake in Utah, that for many square miles there is nothing but a dazzling field of white salt. In other cases where the surface water has evaporated without leaving a surface layer of salt, the subsoil is so saturated with strong brine that most plant life is unable to survive.

The sides of these characteristic Great Basin valleys slope gradually from the bases of the enclosing

mountain ranges. Soil from the mountains is being continually carried down and deposited at the mouths of the canyons where broad alluvial fans are often formed. The mineral salts are leached out from the soils at the bases of the mountain ranges and are carried to the lower-most parts of the valley floors where they are deposited. Thus the salt content becomes so high that all plant growth is prohibited and barren playas are formed. Most every valley has one or more of these playas and they occur even in valleys, such as Pine Valley, which was never covered by Lake Bonneville.

#### MAJOR SHRUB BIOTIC COMMUNITIES

Because of the physiographic features and geological history of the Great Basin there is a wide variation in the climatic conditions and the composition of the soil, both as to texture and mineral content, which results in a corresponding variety of biotic communities. This study is concerned with some of those communities which belong to the Northern Desert Shrub Biome<sup>1</sup> which occurs below the piñon-juniper woodland, and which has been referred to as the "Sagebrush Climax" (Clements 1920; Weaver & Clements 1938), the "Northern Desert Shrub Formation" (Shantz 1925; Shantz & Piemeisel 1940); the "Artemisian Province" (Dice 1939), and the "Upper Sonoran Faunal Area" (Merriam 1898).

The "Northern Desert Shrub Formation" of Shantz includes most of the plant communities of the Great Basin except the greasewood and its associated halophytes which he assigns to the "Salt Desert Shrub (Greasewood) Formation." Clements, on the other hand, lumps the above two associations into the "Atriplex-Artemisia Association" with a large number of consociations.

The climax communities of this biome are characterized by scattered dominant deciduous shrubs accompanied by several species of dominant grasses and a limited number of subdominant under-shrubs and herbs. The number of major permeant influent animals is small, practically all of which range throughout all the communities. The minor influent and subinfluents components are more distinct for each community but in many cases the differences are largely quantitative rather than qualitative ones.

The dominant shrubs are rather similar in general vegetative form and present landscape aspects which are strikingly similar to the casual observer. These communities comprise one of the most extensive types of vegetation in western Utah that occur from the piñon-juniper woodland to the lowermost parts of the valleys. Their southern boundary extends to about the thirty-seventh parallel where it dovetails into communities of the southern desert. In northern Utah, southern Idaho, and southeastern Washington they merge into the Palouse Prairie.

<sup>1</sup> The term biome is used as a synonym of biotic formation which consists of a complex of fully developed and developing biotic communities. The mature communities (associations) of this larger biotic unit (biome) represent the final expression of the plant and animal constituents in response to climate and biotic interactions.

The differentiation between the shrub communities of the Northern Desert Shrub Biome and the grassland associations of the Palouse Prairie is not an abrupt one but there is a tendency for a gradual increase in the abundance of grasses and a decrease in the number of xeric shrubs as availability of moisture increases.

These communities have been referred to as the "Basin Sagebrush Climax" (Weaver & Clements 1938), which is misleading because sagebrush is only one of the important dominant shrubs of the region and is no more conspicuous than shadscale, a fact which is implied by the same authors when they refer to the climax community as "The Atriplex-Artemisia Association." Grasses are also among the important dominants but they have been greatly reduced since the advent of the white man and his domestic animals. The early explorers of the Great Basin (Fremont 1845; Stansbury 1852; Beekwith 1855; Simpson 1859; and Hayden 1873) all record the presence of grass among the vegetation encountered. These early explorers were also prone to refer to a number of different species of shrubs all as "sage," "sagebrush," or "artemisia." This may have been partly responsible for the misconception as to the extensiveness of this species. Greasewood was usually differentiated from sagebrush but not always, and shadscale was often referred to as "sage." These early explorers also probably came in contact with the sage more frequently than some of the other shrubs because they tended to follow the bases of the mountains and streams where they were more likely to find suitable drinking water and where more grass was apt to be present for their animals.

The sagebrush community is only one of the biotic communities of the Northern Desert Shrub Biome and is restricted to those areas where the most moisture is available. Thus sagebrush is usually found at the bases of the numerous mountain ranges or in the valleys where the soil is deep, relatively free from mineral salts, more permeable, and with a greater water-holding capacity; or where there is a greater amount of precipitation, whereas shadscale is restricted to the more xeric areas and/or areas of higher mineral content than is tolerated by sagebrush.

#### LOCATION OF STUDY AREAS

The shadscale association and its closely related communities were studied most intensively in White Valley, located about 65 miles west of Delta, Millard County, Utah (Fig. 1). Observations were also made in Antelope Valley, Snake Valley, Pine Valley, and the eastern slope of the House Range. White Valley is bisected by the 113° 30' W. and extends in a north and south direction from the 39° 00' N. to 39° 35' N. It is a closed basin more than 60 miles in length; about 900 square miles in area; and is bordered on the west by the Confusion Range, which separates it from Snake Valley, and on the east by the House Range, which separates it from the Sevier Desert. The central playa of the valley is about 4,400 feet above sea level and the sloping sides of





the valley gradually rise to an elevation of 5,500 to 6,000 feet at the bases of the enclosing mountain ranges.

The strata of the bordering mountains consist chiefly of Paleozoic limestone and quartzites. In the House Range they dip toward the east, away from White Valley, and their outcropping edges form a steep, rugged west-facing wall which for many miles towers precipitously above the valley. In the northern part of the Confusion Range the dip is toward the east, which is thus toward the valley, with the result that the slope from the mountains to the central valley floor is relatively long and gentle. The valley is thus asymmetrical, the lowest part lying nearer the base of the House Range.

The lowermost part of the valley floor consists of a flat barren playa about 3 miles across at its widest point and 12 miles long. During heavy rains the lowest parts of the valley are flooded with water and are devoid of vegetation. The soil here was formed under water and is a dense gumbo clay so heavily impregnated with mineral salts that they form a white encrustation on its surface, hence the name "White Valley." In some parts, surrounding this lowest area, a miniature eolian topography of innumerable hummocks that range in height up to 12-15 feet is imposed on the landscape. These hummocks consist of residual clay collected and held in place by pickleweed, *Allenrolfea occidentalis* (S. Wats.) Kuntze, whereas the surrounding areas have been lowered by wind erosion (Fig. 10). Toward the south the valley becomes more constricted and trough-like, but its central axis remains low, and with the exception of some interruptions where the entire valley floor is covered with vegetation, it retains its playa character.

This White Valley drainage basin has no permanent stream and only a few springs. A group of small springs, including Coyote, Willow, Tule, and South Tule Springs occur in the low central part of the valley. Most of these springs consist of a circular depression where the water comes to the surface in one place and sinks in another. The water at Tule Springs arises at a point about 375 meters from where it again disappears into the ground. These springs are usually choked with a dense growth of rushes *Scirpus olneyi* A. Gray, and *Juncus balticus* Willd. Some are bordered by a dense growth of willows *Salix exigua* Nutt., and all of them are usually surrounded by a zone of salt grass *Distichlis stricta* (Torr.) Rydb., which often forms a solid sod.

Around the edges of the valley, sloping down from the bases of the surrounding mountain ranges, are deposits from torrential streams in the form of alluvial fans. The material varies from boulders and gravel near the base of the mountains, to sand, loam, or clay at the outer edge of the fan. Such soils vary greatly in depth, are usually productive, well drained and fairly free from alkali.

The area selected for the sagebrush community study is known as "Fernow Valley" and is located

about 15 miles west of Levan, Juab County, Utah, at an elevation of about 5,600 feet (Fig. 1). The valley runs in a north and south direction and drains toward the south. It is hemmed in on the east, north, and southwest by low rocky mountain ranges covered with a piñon-juniper forest into which the sagebrush community extends as a shrub layer. The soils in this valley are largely the result of stream deposition and range from a sandy clay loam along the valley floor to gravel at the bases of the enclosing hills. The soils are deep, well-drained and permeable. Ravines in the south end of the valley indicate that the soil is more than 20 feet in depth.

#### METHODS OF STUDY

The determination of the plant constituents of each community was accomplished by taking 0.25 square rod samples with a quadrat frame whose dimensions were 8' 3" per side. Three cross-wires were strung from the opposite sides of the frame thus dividing it into 16 equal parts. This frame was placed on the ground and the positions and area covered by each plant plotted with reference to the cross-wires. The samples were taken within the plots which were used for sampling rodent populations. Four quadrat samples were taken per trapping plot. From these samples the principal plant components for each community were calculated in terms of percentage of total floral composition, frequency of occurrence in the samples taken, and percentage of total ground surface covered.

One square meter samples of the invertebrate populations of the various dominant shrubs were obtained by making 50 sweeps with an insect net 30 centimeters in diameter. These quantitative collections were taken from sagebrush, greasewood, shadscale, and tetradymia communities at intervals of about 7 to 10 days.

No one method is adequate in estimating vertebrate populations and consequently different methods were used for different groups. The frequency with which the larger mammals such as antelope, coyotes, and badgers were seen and heard, together with the frequency of their "signs," in the form of scat, tracks, dens, and excavations were used as indices of relative abundance.

The relative abundance of rabbits and birds were estimated by staking out 4-hectare (10-acre) plots within which the number of birds and rabbits were counted by walking back and forth across the area until it had been thoroughly covered. The pellet-count method was also utilized in determining differences in the relative abundance of rabbits from one community to another. Each sample consisted of one square meter of ground surface on which the number of rabbit pellets were counted. These random samples were taken at intervals of 25 meters along transects running through the various communities.

The relative abundance of small rodents was estimated by trapping 0.4-hectare (1-acre) and 0.2 hectare (0.5-acre) plots for 4 consecutive nights

Circular plots were used with the traps arranged in 9 circular rows in the 0.4-hectare plots and 6 rows in the 0.2-hectare plots. Traps were spaced 16-18 feet apart and thus made an average of 219 traps per 0.4-hectare plot and 105 traps per 0.2-hectare plot.

Food relations of the various animals were investigated by examining the contents of their stomachs and pellets; by making observations on their feeding activities in the field; and by observing food preferences of captive animals.

The time of reproduction was determined by examination of the reproductive organs of collected animals; by observing the nesting and mating activities of animals in the field; and by observing the time at which the young made their appearance.

The trapping plots described above were also utilized in estimating relative lizard populations. The lizards within a plot were counted as the area was thoroughly covered by making 6 to 7 complete circles at intervals of 5 to 6 meters apart from the outside to the center. Duplications in such counts were guarded against by noting the position and course taken by each flushed specimen. Although the counts obtained by this method probably do not represent the actual number of lizards present, because of the possibility that some were not flushed, yet by employing this method in all the different communities it served to indicate relative differences between them.

Daily temperature and relative humidity data were recorded by means of a hygro-thermograph placed beneath a weather shelter on a platform six feet above the surface of the ground. The temperature recordings were checked against a thermometer at least once a day and the relative humidity recordings against a sling psychrometer reading every two to three days. The rates of evaporation were measured by means of standardized white porous porcelain cylindrical atmometers placed at three different levels. One was placed at 52 inches above the ground (greasewood level); another at 18 inches (maximum shade level); and the third one at ground level.

The scientific names used in the designation of the biotic components encountered in this study follow the nomenclature of the specialists who identified the specimens collected, and the following authorities: "Flora of Utah and Nevada," I. Tidestrom, 1925; "Manual of the Grasses of the United States," A. S. Hitchcock, 1935; "List of North American Recent Mammals, 1923," G. S. Miller, Jr., 1924; "Checklist of the Birds of Utah," William H. Behle, 1944; "A Check List of North American Amphibians and Reptiles," Stejneger & Barbour, 4 ed. 1939; "Insects of Western North America," E. O. Essig, 1934.

The terms and concepts used with reference to the biotic components and their relationships within the various communities are adopted from "Bio-ecology" by Clements & Shelford (1939).

## CLIMATE

### COMPARISON WITH CLIMATE OF SOUTHERN DESERT

Although this biome is referred to as a "desert" biome, its climate is very different from the climate of the southern desert biome in southwestern United States. The term "Northern" is used to denote a semi-desert condition and to differentiate it from the true southern desert.

The differences in the climate of the Southern Desert Scrub Biome and the Northern Desert Shrub Biome are readily discernible from the climographs in Figure 2. Climograph A, that represents the climatic conditions in the southern desert, is based on climatic data taken from United States Weather Bureau reports for eight different weather stations ranging in latitude from Tucson, Arizona to Logandale, Nevada and in elevation from sea level at Calexico, California to 2,033 feet above sea level at Las Vegas, Nevada. Climographs B and C are based on United States Weather Bureau reports from government weather stations the locations of which are described below.

Temperatures are much higher in the southern desert, and reach a maximum of 130-134° F. in the Imperial Valley region with maxima of 110-120° F. of rather common occurrence in other parts of the biome, whereas the maximum for the northern desert biome is about 115° F. and in most places it seldom exceeds 105° F. The annual mean temperature of the southern desert ranges between 60 and 72° F. as compared with 45-50° F. for the northern desert. Minimum temperatures, which are often the critical temperature factors as far as plant and animal distribution are concerned, are strikingly different in the two biomes. Many parts of the southern desert seldom experience frost and in all parts below 5,000 feet the temperatures usually remain above 10° F. as contrasted with minimum temperatures of -20 to -30° F. in the northern desert areas. Such characteristic southern desert plants as *Covillea tridentata* (DC.) Vail, *Strombocarpa odorata* (Torr. & Frém.) Torr., and *Prosopis glandulosa* Torr. have been known to sustain severe frost damage in southern Utah (the northern limit of the southern desert) when, for a period of only 7 days, the temperature abnormally fell to below 32° F. with a minimum of -11° F. for one night (Cottam 1937; Turnage & Hineckley 1938; Woodbury 1938).

The yearly distribution of precipitation in the two biomes is similar in some respects but different in others. Both biomes are characterized by having two wet periods during the year but these periods occur at different times and the proportions of the annual rainfall received during these periods are different (Fig. 2). In the southern desert the wet spring season ends about the last of March and a long dry period follows from April to July, whereas in the northern desert the wet winter and spring period extends into May and the dry summer period lasts only until mid-July or early August.

The annual precipitation of the southern desert

varies from 3-10 inches per year, seldom being more (Smith 1930), whereas in the northern desert it seldom falls below 5 inches, except in the southern part and in periods of drought, and exceeds 16 inches in some sagebrush areas of the northern part of the biome.

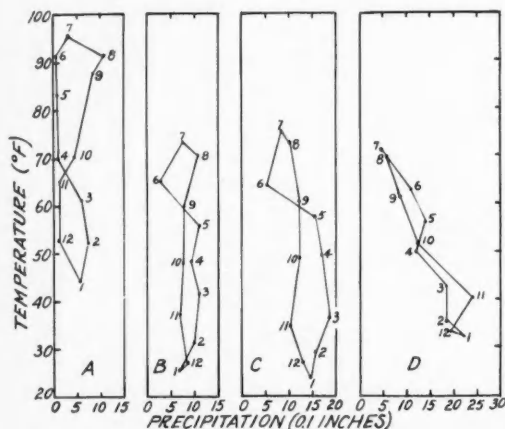


FIG. 2. Climatic diagrams representing the monthly mean temperature-precipitation relationships of: A. Southern Desert Scrub Biome; B. Shadscale Association; C. Sagebrush Association; D. Palouse Prairie (Pomeroy, Washington). Data from U. S. Weather Bureau Reports.

#### SOURCES OF CLIMATIC DATA

Climatic data for the shadscale areas were obtained from United States Government Weather Bureau reports for 6 weather stations located in areas where shadscale and its associated communities are prevalent. These stations are so distributed that the extremes as well as the average climatic conditions are represented. The stations chosen are all within the altitudinal range of 4,000 to 5,000 feet above sea level and are distributed latitudinally from Modena, at the southern extreme and within 60 to 70 miles of the southern boundary of the biome, to Wendover on the north (Fig. 1.). The Wendover station, because of its location at the eastern base of a low mountain range to the northwest, is representative of extremes as to maximum temperatures, low precipitation and minimum snowfall. The other stations are located in a triangular fashion in three different directions from White Valley. The Garrison station is the nearest one to White Valley and is located about 35 miles to the southwest. Precipitation data was also obtained from the Desert Range Experiment Station about 35 to 40 miles south of White Valley and in an intermediate position between the Garrison and Milford stations.

Temperature, relative humidity and evaporation data were recorded at White Valley during the course of the investigation.

Climatic data for sagebrush areas were obtained from the records of four United States Government Weather Bureau stations located at Fillmore, Oak

City, Levan, and Santaquin which range in elevation from 4,900 to 5,250 feet above sea level (Fig. 1). These stations are all located within sagebrush areas situated along the western bases of mountain ranges.

#### TEMPERATURE

Temperature values within the shadscale and sagebrush areas are very similar. The annual range in temperature is very great and may be as much as  $145^{\circ}\text{F.}$ , ranging from a maximum of  $110^{\circ}\text{F.}$  to a minimum of  $-30^{\circ}\text{F.}$  in the shadscale areas and from a maximum of  $115^{\circ}\text{F.}$  to a minimum of  $-28^{\circ}\text{F.}$  in the sagebrush areas. The annual mean temperature is slightly higher in the sagebrush areas varying from  $47.5^{\circ}\text{F.}$  at Levan to  $51.7^{\circ}\text{F.}$  at Fillmore with an average of  $49.9^{\circ}\text{F.}$  In the shadscale areas it varies from  $47.6^{\circ}\text{F.}$  at Modena to  $52.8^{\circ}\text{F.}$  at Wendover with an average of  $49.5^{\circ}\text{F.}$  (Fig. 3). July is the hottest month of the year, with a mean temperature of  $73.7^{\circ}\text{F.}$  for the six stations in the shadscale areas and  $74.6^{\circ}\text{F.}$  for the 4 stations in the sagebrush areas. The monthly mean temperatures during 1939 and 1940 were 1 to 4 degrees above normal, being abnormally high during July and August.

The daily fluctuations in temperature are also very wide, ranging from an average of  $21.5^{\circ}\text{F.}$  in January to an average of  $43.2^{\circ}\text{F.}$  in June, with a maximum range of  $56^{\circ}\text{F.}$  during June, July, and August. Maximum daily temperatures occur from 2 to 6 p.m. and the minimum temperatures from 2 to 4 a.m.

#### PRECIPITATION

The amount of precipitation is much lower in the shadscale areas than in the sagebrush. It varies from an annual minimum of 3.50 inches at the Desert Range Experiment Station to a maximum of 19.06 inches at Modena, whereas the minimum for the sagebrush areas is 7.20 inches and the maximum 26.22 inches. The annual mean precipitation in the shadscale areas varies from 11.01 inches at Modena to 4.53 inches at Wendover with an average of 7.95 inches for the six stations. This is slightly more than half the amount received in the sagebrush areas, which average 14.84 inches per year (Fig. 3).

Sagebrush areas are often located along the windward border of the mountain ranges where the precipitation is higher than it is in the open valleys because the moisture-bearing winds drop their moisture as they rise when the mountains are encountered. Deseret, situated in a large open valley at an elevation of 4,541 feet, 25 miles to the windward side of the Pavant Mountain, has a normal annual precipitation of 8.16 inches, while Fillmore, at an elevation of 5,250 feet and located at the windward base of the mountain, receives an average of 14.30 inches of moisture per year. This difference in precipitation is very markedly reflected in the type of vegetation present; sagebrush is the dominant plant along the base of the Pavant range and shadscale and greasewood in the open valley in the vicinity of Deseret.

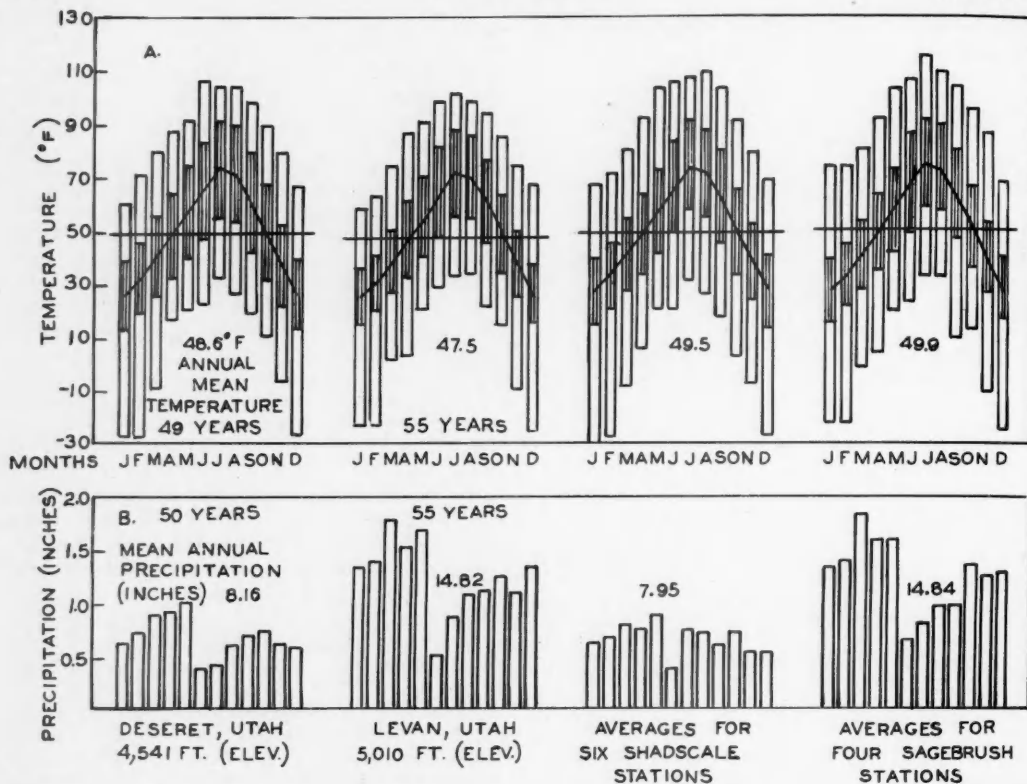


FIG. 3. Temperature and precipitation data for shadscale and sagebrush areas: A. Monthly maxima, minima, means, mean maxima, mean minima, and annual mean temperatures; B. Average monthly precipitation. From U. S. Weather Bureau Reports. Records ended with 1944.

The precipitation is unevenly distributed throughout the year, most of it comes during 2 periods. The wettest period of the year occurs from March to May with March usually receiving the greatest amount in the sagebrush areas and May in the shadscale areas (Fig. 3). June is normally the driest month of the year but during 1939 and 1940 July received the least amount of precipitation. In the shadscale areas the average amount of rainfall during June is only 0.36 inch, varying from 0.20 inch at Garrison to 0.65 inch at Grantsville. In the sagebrush areas the average for June is 0.62 inch. This dry period is normally followed by an increase in precipitation during July and August when the average for the shadscale areas is 0.75 inch with a range from 0.28 inch at Wendover to 1.08 inches at Modena.

The distribution of rain is very uneven as far as the entire region is concerned. The amount of precipitation varies greatly from one station to another. Storms are very localized and on several occasions enough rain may fall in one part of White Valley to cause a considerable run-off, while in another part, 10 to 15 miles away, not a drop falls. Many of the summer storms are "cloudbursts" that

result in a very heavy downpour which may last for only a few minutes. The utilization of this summer precipitation is often very low because it is temporary and available to the plants for only a short time. The suddenness and intensity of such thunder showers, together with the sloping topography of much of the terrain and the sparseness of the vegetation, results in a heavy run-off, especially in the shadscale areas. What moisture does soak into the soil does not penetrate to very great depths and is soon lost by evaporation because of the high temperatures, low relative humidity, and high wind velocities. Thus the soil surface moisture, that results from a storm, may be dissipated within a few hours after the storm is over.

The plants of both the shadscale and sagebrush areas are subjected to great variations in the amount of precipitation they receive from one year to the next. During the 25-year period from 1920 to 1944 such yearly variations amounted to as much as 6.78 inches at Deseret, Utah and 13.11 inches at Levan, Utah (Fig. 4). The annual precipitation of the sagebrush areas very seldom falls below the annual mean of the shadscale areas.

The sagebrush areas receive more than twice the



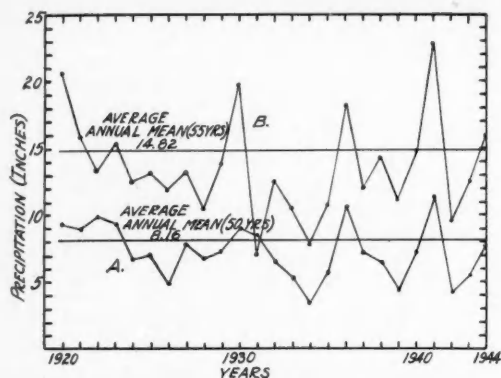


FIG. 4. Fluctuations in annual precipitation during a 25-year period from 1920 to 1944, inclusive, at: A. Deseret, Millard County, Utah; B. Levan, Juab County, Utah. Data from U. S. Weather Bureau Reports.

amount of snow that is received in the shadscale areas. The average annual snowfall varies from 45.5 inches at Oak City to 78.6 inches at Fillmore with an average of 66.2 inches for the 4 stations, as compared with an average of 27.2 inches for the stations in the sagebrush areas where the range varies from 8.8 inches at Wendover to 33.9 inches at Milford (Table 1).

TABLE 1. Average monthly and annual snowfall in inches (Kincer 1936).

Stations	Length of Record	SHADSACLE AREAS											
		January	February	March	April	May	September	October	November	December	Annual		
Deseret.....	33 yr.	5.2	7.0	4.9	2.7	0.1	0.1	0.5	2.4	5.3	28.2		
Grantsville.....	18 "	9.0	6.1	4.4	2.3	T <sup>2</sup>	0	1.2	2.9	7.8	33.7		
Milford.....	20 "	6.3	6.8	5.2	3.8	0.9	T	0.3	4.0	6.6	33.9		
Modena.....	30 "	6.8	6.5	6.4	2.7	1.0	T	1.4	2.7	4.0	31.5		
Wendover.....	18 "	2.3	1.6	0.7	T	T	0	T	1.0	3.2	8.8		
Average.....		5.9	5.6	4.3	2.3	0.4	T	0.7	2.6	5.4	27.2		
SAGEBRUSH AREAS													
Fillmore.....	16 "	14.7	13.3	14.2	8.6	0.6	0	4.3	8.5	14.4	78.6		
Levan.....	38 "	12.6	12.4	13.1	5.9	1.2	0.2	2.3	6.7	13.2	67.6		
Oak City.....	18 "	9.5	7.2	8.4	4.4	0.2	T	1.8	5.1	8.9	45.5		
Santaquin.....	15 "	17.2	15.2	11.5	6.0	T	T	1.5	6.6	15.2	73.3		
Average.....		13.3	12.0	11.1	6.2	0.5	T	2.5	6.9	12.2	66.2		

<sup>2</sup>Trace.

#### LENGTH OF GROWING SEASON

The frost-free period averages 120 days in the shadscale areas and about 136 in the sagebrush areas, and extends from about May 20 to September 20 in the shadscale areas and from May 18 to October 1 in the sagebrush areas. The number of clear days per year averages 181 with a maximum of 19 in June, the driest month of the year. The annual sunshine percentage amounts to 74 at Modena with a maximum of 86 during the month of June (Kincer 1936).

#### WIND

Scarcely a day passes without the wind blowing. This air movement reduces the intensity of the high summer temperatures but it also increases the rate of evaporation to which the plants are subjected. The average hourly wind movement is 11.5 miles at Modena, being highest during May and June. Monthly maximum velocities vary from 44 to 53 miles per hour (Kincer 1936).

#### RELATIVE HUMIDITY AND RATES OF EVAPORATION

The annual average relative humidity, based on the average of 3 readings taken at 8:00 a.m., noon, and 8:00 p.m., are 46% for Modena and 49.6% for Salt Lake City.<sup>3</sup> The relative humidity is lowest during June and July when the minimum monthly average drops to 26.6% at Modena and 33.3% at Salt Lake City. The highest percentage occurs during the winter months when it reaches 79% at Modena and 75% at Salt Lake City (Kincer 1936).

At White Valley the maxima occurred in early morning between 2:00 and 6:00 a.m. and the minima during late afternoon from 2:00 to 6:00 p.m. The daily maxima fluctuated considerably and seldom got above 60% during the spring and summer except during rain storms. The mean minimum during July, 1940 was 20.3% with a range from 3% to 31%. Monthly means for June and July were 28.3% and 30.2% respectively.

Evaporation is moderately heavy because of the dry atmosphere and the high wind velocities during the afternoon when temperatures are highest and relative humidity lowest. The average loss of water from the Weather Bureau pan is about 60 inches (Table 2). Pan losses frequently exceed 10 inches a month during June, July, and August and have exceeded 12 inches several times. The greatest loss was 16.75 inches in July, 1928. The evaporation-precipitation ratio varies during the summer months from 8.50 in April to 37.02 in June (Table 2).

TABLE 2. Average monthly and annual evaporation and precipitation data (inches) for Sevier Bridge Dam, Juab County, Utah; located about 13 miles southwest of Levan and 15 miles east of Oak City. (Compiled from Kincer 1936.)

	Length of Record	April	May	June	July	Aug.	Sept.	Annual
Evaporation....	9 years	4.847	9.827	12.588	13.652	10.858	7.967	59.739
Precipitation....	9 "	0.57	0.82	0.34	0.85	1.28	0.71	8.49
Evap. / Prec.....		8.50	11.98	37.02	16.06	8.48	11.22	7.03

Evaporation rates from standardized atmometers set up in the shadscale association in White Valley varied considerably at different levels and at different times of the day, being highest during the afternoon hours. The average rate during 15 weeks of observation from April 16 to July 16, 1940, was 3 milliliters per hour at the 52-inch level; 2.25 milli-

<sup>3</sup> Data for Salt Lake City is used because no data on relative humidity is available for the other stations in the vicinity of the sagebrush area studied.

liters at the 18-inch level; and 2.18 milliliters at the ground level, with an average weekly range from 1.33 milliliters per hour at the ground level in April to 4.41 milliliters at the 52-inch level in June. The absolute range varied from a minimum of 0.6 milliliters to a maximum of 7.22 milliliters per hour.

The rate of evaporation is greatly affected by air movement since there was a definite increase in the rate from the ground level to a height of 52 inches. Although the temperature at the ground level gets higher than at the higher levels, the effect of this factor in increasing the rate of evaporation is evidently more than compensated for by the increased air movement at the higher levels (Fig. 5).

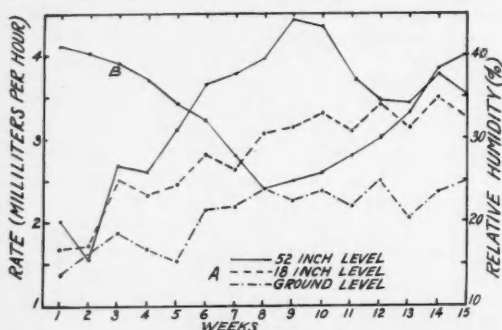


FIG. 5. Evaporation and relative humidity during a 15-week period from April 16 to July 16, 1940 at White Valley, Millard County, Utah: A. Evaporation rates in milliliters per hour from standardized atmometers placed at three levels; B. Average weekly relative humidity.

The taller plants, such as greasewood, may be subjected to much greater water losses through increased transpiration than those that grow at lower levels because of this higher evaporating power of the air. This may be a very important factor in the distribution of the greasewood which is found almost exclusively in the lower parts of the valleys where the water table is higher and consequently where more moisture is available. When this plant occurs on the higher ground it seems to suffer more from drought than the other plants of such areas and is frequently killed.

#### BIOTIC MATRIX OF THE SHADSCALE AND ASSOCIATED COMMUNITIES

The dominants of these desert communities receive the full impact of a very rigorous climate and modify the various aerial factors, especially moisture and insolation, to which all the biotic components are exposed. The combination of dominants and subdominants also impart character to the community and play an important role in the food relationships, shelter and reproduction of the influent animals. The invertebrate animals (subinfluents) constitute the basic reactors and coactors within the communities and form the basis of the food chains of many of the larger animals. Thus, the plants because of

their importance as dominants and subdominants, together with the invertebrate animals constitute the "biotic matrix" of the community which serves as a foundation and framework, on and into which, the larger influent animals fit.

Although the major and minor influents are an integral part of the community and through their coactions and reactions directly or indirectly affect the composition and structure of the biotic matrix, they are discussed by the writer in a separate section of this paper, in order to avoid repetition since many of them occur in more than one community.

#### THE SHADSCALE COMMUNITY

##### (*Atriplex-Oryzopsis-Dipodomys* Association)<sup>4</sup>

**Dominants and subdominants**—Shadscale is very widely distributed throughout the Great Basin being most prevalent in the more xeric parts. It is well adapted to xeric conditions and occurs where the precipitation is considerably less than where sagebrush is found or where the mineral content of the soil is beyond the tolerance of the sagebrush. The soil on which it occurs is rather impervious and the ground sloping so that the run-off is high. Thus the available moisture supply is low and is largely limited to the surface soil. This plant has an extensive root system near the surface as well as a taproot and can thus utilize the temporary surface moisture supply, thriving very well even though its roots may be able to penetrate the soil to a depth of only 1 or 2 feet. This characteristic also enables it to occupy areas where the subsoil is rather heavily impregnated with mineral salts. Although it is relatively salt-tolerant, and occurs in areas where the salt concentration may be as much as 1.15 percent at the 3-foot level, it thrives best where the salt content of the soil does

TABLE 3. Floral components of 40 quadrat samples taken in Shadscale Community. 1, Percent of samples in which the species occurred; 2, Number of plants per square rod; 3, Percent of total plants in samples; 4, Percent of ground surface covered.

Species	1 Frequency	2 Abundance			3 Composition			4 Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Atriplex confertifolia</i> ..... (Torr. & Frém.) S. Wats.	100.0	180	20	50.8	81.1	17.4	43.0	15.4	1.6	7.4
<i>Eurotia lanata</i> ..... (Pursh) Moq.	80.0	108	0	38.8	77.2	0	32.6	5.5	0	1.7
<i>Artemisia spinescens</i> ..... D. C. Eaton	72.5	76	0	10.0	59.4	0	9.4	2.0	0	0.4
<i>Oryzopsis hymenoides</i> ..... (Roem. & Shult.) Ricker	32.5	56	0	1.1	43.3	0	2.8	4.2	0	0.5
<i>Hilaria jamesii</i> ..... (Torr.) Benth.	30.0	24	0	1.1	27.8	0	4.9	5.5	0	0.8
<i>Sphaeralcea grossulariifolia</i> ..... (Hook. & Arn.) Rydb.	25.0	24	0	0.8	22.2	0	3.3	1.2	0	0.1
<i>Tetradymia glabrata</i> ..... A. Gray	12.5	4	0	0.5	5.0	0	0.5	1.6	0	0.1
<i>Sporobolus cryptandrus</i> ..... (Torr.) A. Gray	7.5	12	0	1.0	18.5	0	1.0	0.5	0	0.03
<i>Chrysothamnus stenophyllus</i> ..... (A. Gray) Greene	7.5	4	0	0.3	4.5	0	0.2	2.5	0	0.07
<i>Kochia vestita</i> ..... (S. Wats.) Rydb.	7.5	40	0	6.0	10.0	0	2.1	2.4	0	0.07
<i>Ephedra nevadensis</i> ..... S. Wats.	5.0	8	0	0.1	9.0	0	0.3	8.1	0	0.03

<sup>4</sup> Each community is technically designated by the names of two dominant plants and one prevalent influent animal.

not exceed 0.09 percent (Kearney, Briggs, Shantz, *et al.* 1914, and Shantz 1925).

This community occupies about 20 to 30 percent of the vegetated part of White Valley. In most places it extends from near the bases of the mountain ranges to near the valley floors where it becomes associated with greasewood forming an ecotone community in some areas. Within this ecotone community shadscale and greasewood occur in about equal abundance; greasewood predominates in the lower areas and shadscale in the higher areas. Here gray molly, *Kochia vestita* (S. Wats.) Rydb., reaches its maximum abundance. This is a small subdominant perennial which occurred in large numbers in certain areas, 308 plants per square rod, but its coverage was always small on account of its small size (Table 3). It is favored by over-grazing and becomes most abundant where the shadscale has been depleted or not present because of unfavorable soil conditions.

TABLE 4. Floral components of 16 quadrat samples in *Atriplex-Sarcobatus* Ecotone.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Atriplex confertifolia</i> .....	100.0	48	12	22.8	48.0	4.5	13.8	7.3	1.6	4.0
(Torr. & Frém.) S. Wats.										
<i>Kochia vestita</i> .....	100.0	308	40	161.6	85.0	40.0	69.9	7.2	1.0	3.6
(S. Wats.) Rydb.										
<i>Artemisia spinescens</i> .....	75.0	40	0	22.0	25.6	0	8.0	2.1	0	0.7
D. C. Eaton										
<i>Eurotia lanata</i> .....	75.0	36	0	12.8	23.1	0	6.8	2.2	0	0.7
(Pursh) Moq.										
<i>Sarcobatus vermiculatus</i> ...	37.5	8	0	1.0	3.5	0	0.9	4.4	0	1.1
(Hook.) Torr.										
<i>Hilaria jamesii</i> .....	12.5	12	0	1.6	4.7	0	0.6	0.6	0	0.07
(Torr.) Benth.										

Shadscale is usually accompanied by one or more dominant grasses including Indian rice grass, *Oryzopsis hymenoides* (Roem. & Shult.) Ricker and galleta grass, *Hilaria jamesii* (Torr.) Benth. Sand dropseed, *Sporobolus cryptandrus* (Torr.) A. Gray, is present in certain areas. Blue gramma grass, *Bouteloua gracilis* (H. B. K.) Lag., occurs with shadscale in Pine Valley in rocky situations (Stewart, Cottam, & Hutchings 1940). The dominant grasses seldom occur in pure stands and where they do the areas are small. The testimonies of old residents of the region indicate that the abundance of grass has been reduced by grazing but that the characteristic desert shrubs, such as shadscale, have always been abundant. Indian rice grass is one of the most conspicuous grasses where the soil is sandy and under protected conditions it becomes abundant enough to alter the general landscape aspect of the community (Fig. 7).

Two of the subdominant shrubs associated with shadscale are winterfat, *Eurotia lanata* (Pursh) Moq., and bud sage, *Artemisia spinescens* D. C. Eaton, which is most conspicuous during the early spring. Bud sage is the only artemisia of the area which reproduces in the spring of the year. During



FIG. 6. Shadscale community on east side of White Valley, Millard County, Utah. (May 31, 1940.)

early summer it loses its leaves and dries up to the extent that it appears to be practically dead. In early spring months it is highly palatable and has consequently been reduced by grazing.

Jointfir, *Ephedra nevadensis* S. Wats., is found scattered about in the shadscale community near its upper limits but it seldom becomes abundant. It occurred in only 12.5 percent of the quadrat samples and constituted only 0.5 percent of the vegetative composition of this community.



FIG. 7. Shadscale community within an enclosure protected from grazing at the Desert Range Experiment Station, Pine Valley, Millard County, Utah. Note the abundance of Indian rice grass among the shadscale. (Aug. 9, 1940.)

In early spring a number of annual and perennial herbaceous plants make their appearance. These were never abundant and many of them were restricted to the more open areas. Such seasonals included the globemallow, *Sphaeralcea grossulariaefolia* (Hook. & Arn.) Rydb.; the larkspur, *Delphinium bicolor* Nutt.; the evening star, *Montzelia albicaulis* Dougl., which occurred on very gravelly soils; the evening primrose, *Sphaerostigma utahense* Small, usually on sandy soil; *Chylisma scapoidea* (Nutt.) Small, on very gravelly and sandy soils; princees plume, *Stanleya arcuata* Rydb., which was

never very abundant but was conspicuous because of its height and long yellow inflorescence; the umbrella plant, *Eriogonum hookeri* S. Wats., which readily came in where other vegetation had been removed and which was often conspicuous along the sides of newly constructed roads; the silver plant, *Eriogonum ovalifolium* Nutt.; the ragwort, *Senecio uintahensis* (A. Nels.) Greene; and the Russian-thistle, *Salsola pestifer* A. Nels., which readily invaded disturbed areas.

*Invertebrates of the Shrub Layer Society*<sup>5</sup>—Only two layer societies are found in most of the biotic communities of the desert because of the paucity of herbs. The few herbs which are present usually occur as scattered individual plants and seldom form a cover of sufficient extent to form an intermediate layer between the shrubs and the ground. In White Valley the invertebrate population of the shrub layer was much smaller than in either the greasewood or tetradymia communities and reached its peak during the middle part of May (Fig. 9). Since the shade-scale plants are smaller and widely scattered their ground coverage averaged only about half as much as tetradymia or greasewood. Consequently the actual amount of vegetation covered by a sweep net in taking quantitative samples would tend to be less even though the total area covered by the net would be theoretically the same. This may have been one factor partly responsible for the apparent low invertebrate population.

After about the middle part of June the invertebrate populations rapidly began to decrease and by August very few invertebrates were taken in quantitative sweepings. This decrease coincided with a rise in temperature and a lack of precipitation which reached abnormal proportions during July and August 1940.

Spiders were taken more consistently throughout the summer than any other invertebrate but constituted less than 10 percent of the total invertebrate population. Most of those taken during the late summer were immature. The most abundant species were *Philodromus* sp., *Metepeira foxi* Gertsch and Ivie, and *Misumenops celer* (Hentz).

Mites often occurred in aggregations on certain plants but were not taken consistently in quantitative samples. Eighty-six specimens of *Atomus arvensis* Bks. were taken in one sample while no more than two mites were taken in any other samples throughout the summer and they occurred in less than 25 percent of the total samples taken.

Homoptera occurred in greater abundance and with greater frequency than any other group of insects (Table 8). Cicadellids were the most numerous and most frequently encountered members of this group with *Eutettix insanus* Ball and *Aceratagallia cinerea* (O. & B.) being the most prevalent species. Fulgorids, aphids, and coccids were also important homopterans. The most abundant fulgorids were *Oecleus fulvidorsum* Ball and *Orgerius minor* Ball.

<sup>5</sup> The term "society" designates a stratal or layer subdivision of a climax community.

The homoptera are not only important in the biotic matrix of this society because of their coactions concerned with sucking the plant juices but they are also utilized to a great extent as food by lizards and birds.

Although hemiptera constituted more than 15 percent of the total invertebrate population they were not consistently taken in collections. They were most abundant during the middle of May and were occasionally taken until September. Only six species were collected of which the mirids, *Psallus* spp. and *Phyllopidea* sp., were the most abundant. *Phyllopidea* sp. was collected in no other community.

Diptera and hymenoptera occurred in about equal abundance and were much less numerous than in the greasewood community. The 2 most common families of flies were the Bombyliidae and Chloropidae. Robber flies were frequently seen but on account of their agility were seldom taken in the quantitative sweepings. The most common species were *Erax* sp. and *Diogmitis symmachus* (Lw.). The hymenoptera consisted primarily of parasitic wasps and ants. The last of which were seldom taken in quantitative samples although they were very common on the ground. Mutillids were attracted to lights at night but were never taken in the quantitative samples. The most common species was *Brachycistis washingtonia* Mallock.

Lepidoptera and orthoptera were less abundant than most other orders of insects and the frequency of their occurrence was far less than in any other community. Moths were frequently seen at night but were seldom taken in the sweepings. Although grasshoppers were present throughout the summer they were never abundant and were more often seen on the ground than on the vegetation. *Xanthippus lateritius* Saussure, was most frequently seen during April and May, both adults and nymphs being present at that time. *Trimerotropis p. pallidipennis* (Burm.) and the small clear-winged grasshopper, *Acroplus t. tenuipennis* Seudder, were most common during May. Two species of mantis, *Litaneutria minor* (Seudder) and *Stagmomantis* sp., were occasionally seen but practically never taken in the quantitative samples.

Coleoptera were very important members of this society. Eleven species belonging to 7 different families were taken in the quantitative samples. The family Cleridae was the most numerous. Two coccinellids, *Erochomus septentrionis* Ws. and *Hyperaspis fimbriolata* (Melsh.); one clerid, *Hydnocera discoidea* Lec.; the tenebrionid, *Sphaeriontis muricata* (Lec.), and the scarabaeid, *Diplotaxis* sp., were encountered at night but were never taken in the quantitative samples. Two buprestid beetles, *Acmaeodera pulchella immaculata* Horn and *A. pulchella* (Hbst.), were collected from red cloth trap markers placed in the shade-scale but they could never be found on the vegetation. From June 4 to June 12 as many as 7 of these beetles were found on some flags. The scarabaeids, *Cyclocephala reflexa* Csy. and *Polyphylla arguta* Csy., were also members



TABLE 5. Summary of the invertebrates collected in quantitative samples.

	FAMILIES					GENERA					SPECIES					SPECIMENS				
	Shadscale	Tetradymia	Greasewood	Sagebrush	Total	Shadscale	Tetradymia	Greasewood	Sagebrush	Total	Shadscale	Tetradymia	Greasewood	Sagebrush	Total	Shadscale	Tetradymia	Greasewood	Sagebrush	Total
Araneida.....	4	5	6	5	6	8	8	14	9	16	10	10	19	11	23	32	29	138	91	290
Acarina.....	2	3	3	1	4	3	4	3	1	5	4	4	3	1	6	94	42	20	3	159
Collembola.....	1	1	0	0	1	1	2	0	0	2	1	2	0	0	2	3	5	0	0	8
Orthoptera.....	1	1	1	1	1	3	3	2	2	4	3	3	2	5	7	6	8	16	43	73
Thysanoptera.....	0	1	1	0	1	0	2	1	0	3	0	2	1	0	3	0	180	2	0	182
Hemiptera.....	4	4	7	7	8	6	7	14	13	23	6	12	17	15	31	64	635	98	193	990
Homoptera.....	4	3	6	5	9	11	7	14	14	30	13	8	15	16	35	96	123	832	766	1817
Coleoptera.....	7	4	7	7	9	10	7	12	15	21	11	7	13	18	31	19	29	132	193	373
Lepidoptera.....	1	4	4	3	8	*	*	*	*	*	*	*	*	*	*	2	9	14	6	31
Diptera.....	7	8	14	5	17	9	9	16	6	22	9	9	19	7	27	39	85	229	81	434
Hymenoptera.....	3	5	7	5	12	6	9	13	9	24	7	9	18	10	32	33	30	146	17	226
Totals.....	34	39	56	39	76	57	58	89	69	150	64	66	107	83	197	388	1175	1627	1393	4583

\*Larvae and pupae which were not determinable to species.

of this society although they were not taken in the quantitative samples.

The ground layer society—Tenebrionid beetles were very conspicuous components of this society, *Eleodes hispidabris* (Say), *E. hirsuta* Lee., and *E. obscura* (Say) being the most common species. They were most abundant in late spring and early summer at which times they were active both day and night. During the hottest part of the summer they were much less conspicuous and were most active at night. The largest species of the group, *Eleodes obscura*, was very widely distributed and occurred in all communities.

Ants are very important members of these arid regions and through their burrowing activities they perform similar reactions in soil formation that are credited to the earthworm in more moist areas. They are also an important source of food for many lizards, especially the horned-toads (Table 29). The 2 most abundant species were the harvester ant, *Pogonomyrmex occidentalis* (Cress.) and the honey ant, *Myrmecocystus mexicanus navajo* Whlr. Both of these species utilized small pebbles in the construction of their mounds which were most conspicuous where the soils were moderately gravelly. The honey ant was largely restricted to the shadscale, winter-fat, and tetradymia communities but the harvester ant occurred throughout all communities. Other species included *Dorymyrmex pyramicus* (Roger), *Eciton* (*Acamatus*) sp. and several species of *Formica* (Appendix B).

Although grasshoppers probably belong more specifically to the shrub layer where they feed, they occurred very commonly in the open areas where there was no vegetation and where they deposited their eggs. The 4 most common species include *Trimerotropis p. pallidipennis*, *Xanthippus lateritius*, *Aeoloplus t. tenuipennis*, and *Capnobotes occidentalis* (Thomas). Other orthoptera such as

crickets are primarily nocturnal and consequently were much less conspicuous. These included the field cricket, *Gryllulus assimilis* (Fabr.), the camel cricket, *Ceuthophilus fossor* Hubbel, and the sand cricket, *Stenopelmatus fuscus* Haldeman. The field cricket was very scarce being restricted to the more moist situations. The camel cricket was usually found beneath stones and only infrequently seen at night. The large sand cricket was quite common at night, especially in areas where the soil was sandy, and it was readily attracted to mammal traps baited with oatmeal.

Nocturnal arachnids including the scorpion, *Vejois borealis* (Girard), the solpugid, *Eremobates pallipes* (Say), and the tarantula, *Aphonopelma melanius* C. and I., were only occasionally seen because of their secretive habits.

#### THE TETRADYMIA COMMUNITY

##### (*Tetradymia-Atriplex-Dipodomys Faciation*)<sup>a</sup>

Ecological status—Under varying conditions of soil texture, salt content of the subsoil, the presence or absence of a hard-pan, topography, and level of the water table, the composition of the vegetation changes to such an extent that a number of distinct communities are differentiated in which shadscale plays a minor role and some of its associates become the most abundant. Although these communities are all subject to similar climatic conditions, as far as precipitation and temperature are concerned, the availability of the precipitation is altered by the chemical and physical factors which have been described. Whether the water is limited by decreased amounts of precipitation or whether its availability

<sup>a</sup>The term "faciation" is used to designate a biotically distinguishable variation of an association due to the addition or disappearance of one or more dominants. Such additions or deletions are induced by the response of the dominants to alterations in climatic factors. In the area under consideration these alterations in the climatic factors are due primarily to differences in available soil moisture resulting from differences in mineral content and texture of the soil.

to the plants is limited by the soil texture or the mineral content of the soil, the effects on the plant life are essentially the same. Most of these variations of the shadscale association are edaphic communities whose distribution is discontinuous and localized.

The differences which occurred in the floral components were accompanied by differences in the composition of the animal components. Because of the individuality of these biotic communities, although they are subjected to the same climate as the shadscale community, they are herein regarded as climax variations (faciations) of the shadscale association.



FIG. 9. *Tetradytmia* community near base of the House Range on the east side of White Valley, Millard County, Utah. Note coarse texture of the soil and the mixture of the larger *tetradytmia* and smaller shadscale shrubs. (May 18, 1940.)

**Dominants and subdominants**—As the shadscale community extends towards the base of the mountains, *Tetradytmia glabrata* A. Gray, becomes the most prevalent dominant. This community was largely limited to the higher bench lands of the valleys being most extensive on the more gentle slopes. In general it occurred at higher elevations than the shadscale community. It was far more extensive on the west side of White Valley where the slope is more gradual than on the east side. A very extensive area also occurred on the east side of the House Range where the slope is long and gentle.

The soil texture of areas on which this community occurred was usually very coarse varying from large boulders to gravel, however sandy areas occurred to a limited extent. The landscape aspect is quite different from the typical shadscale community, due to the increased height of the *tetradytmia*, and is readily recognizable (Fig. 8). The average ground coverage of the vegetation was much greater, being 21.2 percent as compared with an average of 11.0 percent for the shadscale community.

Eight species of plants occurred in the quadrat samples taken in White Valley, among which were the following dominants: *tetradytmia*, shadscale, Indian rice grass, and galleta grass. The subdominants included the little rabbitbrush, *Chrysothamnus*

TABLE 6. Floral components of 24 quadrat samples taken in the *Tetradytmia* Community.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Tetradytmia glabrata</i> .....	100.0	48	8	23.2	83.3	20	47.2	34.9	8.4	14.5
A. Gray										
<i>Atriplex confertifolia</i> .....	75.0	48	0	8.4	52.2	0	9.2	8.2	0	1.7
(Torr. & Frém.) S. Wats.										
<i>Chrysothamnus stenophyllus</i> .....	50.0	24	0	8.0	66.7	0	19.7	8.9	0	2.1
(A. Gray) Greene										
<i>Hilaria jamaicensis</i> .....	41.7	76	0	9.2	61.3	0	14.2	4.0	0	0.7
(Torr.) Benth.										
<i>Ephedra nevadensis</i> .....	41.7	4	0	1.6	16.7	0	3.5	7.1	0	1.9
S. Wats.										
<i>Eurotia lanata</i> .....	33.3	8	0	0.4	11.2	0	2.5	0.4	0	0.08
(Pursh) Moq.										
<i>Aristida fendleriana</i> .....	25.0	8	0	1.6	15.4	0	2.4	1.8	0	0.2
Steud.										
<i>Artemisia tridentata</i> .....	8.3	4	0	0.8	3.8	0	0.3	0.5	0	0.04
D. C. Eaton										

*stenophyllus* (A. Gray) Greene, bud sage, prickly pear, *Opuntia* sp., globemallow, Indian paint brush, *Castilleja* sp., jointfir, three-awn grass, *Aristida fendleriana* Steud., squirrel-tail grass, *Sitanion jubatum* J. G. Smith, and triodia grass, *Triodia pilosa* (Buekl.) Merr. Along the sides and bottoms of ravines, rabbitbrush, *Chrysothamnus nauseosus* ssp., and big sagebrush extended into this community. The spiny hop-sage, *Grayia spinosa* (Hook.) Moq., occurred on sandy areas. On the east side of the House Range where grazing had been quite severe the little rabbitbrush had become very abundant.

**Invertebrates of the shrub layer society**—Insect populations were much greater than in either the greasewood or the shadscale communities until about June 20 after which time they declined very rapidly (Fig. 9). This large population was made up primarily of hemiptera and thysanoptera which were attracted to the flowers of the *tetradytmia* plants during May and early June. The areas on which this community occurs were usually very rocky and well drained so that as the summer drought began and temperatures rose these plants were subjected to the most xeric conditions of the region. In response to these conditions the seeds were rapidly matured and shed and most of the leaves fell off, with the result that during midsummer these plants were often merely a mass of dry stems and appeared as if they were practically dead. The rapid decline in the insect populations was very strikingly reflected in the seasonal change of this plant, very few insects occurring on it after the first part of July (Fig. 9).

The mirids were the most numerous hemiptera. They were represented by 8 species, of which *Lygus elisus* Van D. and *Psallus* sp. occurred in greatest abundance and with the greatest frequency. Nymphs of *Lygus elisus* were most abundant during the last part of May. False chinch bugs of 2 species, *Nysius ericae* (Schilling) and *N. californicus* Stal., also occurred in considerable numbers.

Homoptera were fairly numerous. Eight species were collected, of which 6 were cicadellids. The most abundant and frequently collected species was *Cera-*

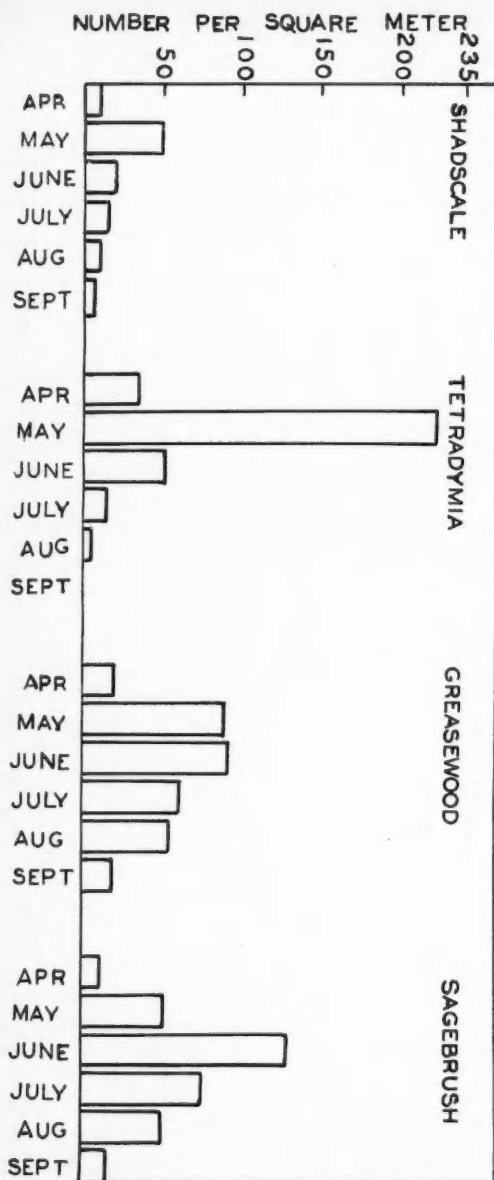


FIG. 9. Seasonal fluctuations in insect populations of the dominant shrubs of the shadscale, tetradymia, greasewood, and sagebrush communities.

*tagallia artemisia* Oman. Other homopterans included the chermid, *Paratrioza cockerelli* (Sule.), and one species of fulgorid, *Oecleidius nanus* Van D., neither of which occurred in samples from other communities.

Coleoptera consisted chiefly of Chrysomelidae. The most abundant species was *Monoxia* sp. Two species of snout beetles, *Eupagoderes varius* Lec. and

*Cercopeus artemisiae* Pierce, also occurred here, the second one being taken in no other community. During the early part of April the June beetle, *Paracotalpa granicollis* (Hall), was very conspicuous, being most abundant on the scattered jointfirs.

Diptera were rather scarce and constituted less than 10 percent of the total invertebrate population. The most abundant species were *Oscinella* sp. and *Madia* sp.

Lepidoptera were very scarce. Only 9 larvae were taken in all the quantitative samples.

Hymenoptera were also few in number. Only 4 species of ants and 5 species of parasitic hymenoptera were taken in the quantitative samples during the entire period of investigation. The most prevalent ants were *Dorymyrmex pyramicus* (Roger) and *Myrmacocystus* sp. Four of the 5 species of parasitic hymenoptera were taken in no other community. The 2 most abundant species were *Leptacis* sp. and *Platygaster* sp.

The grasshoppers included *Melanoplus* sp. and *Aeoloplus t. tenuipennis*, the first species being the more numerous. Nymphs of *Melanoplus* sp. appeared almost a month earlier than they did in the greasewood community, probably because of the more arid and warmer conditions prevailing here. Other orthopterans include the walking stick, *Pseudoserymle straminea* (Seudder) and the mantis, *Litanentria minor*.

Colembola belonging to the genus *Duerosminthurus* made their appearance during the early part of May. During the time of flowering a small yellow thrips, *Frankliniella occidentalis* Perg., was very abundant on the flowers of the tetradymia.

Spiders occurred rather regularly in the samples until about the middle of August but they were never abundant. Of the 8 species collected *Metopcia foxi* and *Misumenops celer* were the most abundant. *Araneus carbonarius* (C. Koch) was very conspicuous because of its webs which extended from one plant to another. Four species of mites were found to be present, the most abundant of which was *Bryobia praetiosa* Koch.

*The ground layer society*—The ants were among the most prevalent subinfluents of this society and were practically the same species as occurred in the shadscale community, with the honey ant and the harvester ant being the most common. Other than ants, the remaining invertebrate composition consisted primarily of orthoptera and coleoptera. Three species of grasshoppers, *Xanthippus lateritus*, *Eremiacris pallida* (Bruner), and *Melanoplus m. mexicanus* (Saussure), were common, especially during the early part of the summer in the most open parts of the community. The sand cricket was common where the soil conditions were suitable. Tenebrionid beetles were common but not so abundant as in the greasewood community. Three species, *Eleodes longicollis* Lec., *E. hispilabris*, and *E. obscura*, were the most prevalent, the first one of which was observed in no other community.

## THE GREASEWOOD COMMUNITY

*(Sarcobatus-Suaeda-Reithrodontomys Faciation)*

Although greasewoods may occur on sand dunes and sometimes at higher elevations in association with shadscale and rabbitbrush or sagebrush, they normally require conditions where considerable amounts of soil moisture are available. When they do occur at these higher elevations, where the water table is low, they are often killed during periods of drought. White (1932) found that in the Escalante Desert the largest areas of greasewood occur where the depth of the water table is less than 15 feet, though at the upper limits of its range the water table may be 25 feet below the surface. The occurrence of this plant at these occasional higher elevations is due to the development of a long taproot which penetrates the soil to depths where water is available. Their roots have been found to extend down 20 to 57 feet below the surface of the soil (Meinzer 1927). Although this species usually occurs on saline soils it is not an infallible indicator of high salt content. Alkali is not necessary for its growth but a high moisture content in the soil is, and inasmuch as the water table is much nearer the surface in the bottoms of the valleys than at higher elevations this plant is largely restricted to such situations even though the salt content of the soil may reach 1.08 percent in the third foot below the surface (Shantz and Piemeisel 1940). When the salt content gets much higher than one percent this shrub becomes yellow and dwarfed and gives way to salt grass, *Distichlis stricta* (Torr.) Rydb., *D. spicata* (L.) Greene, pickleweed, *Allenrolfea occidentalis* (S. Wats.) Kuntze, or samphire, *Salicornia utahensis* Tidestrom, depending on the locality.



FIG. 10. Hummocks of pickleweed (*Allenrolfea occidentalis*) bordering the barren playa in White Valley, Millard County, Utah. (Aug. 10, 1939.)

In White Valley the entire valley floor, except the barren playa and its border of pickleweed, was occupied by this community (Fig. 10). The greatest expanse occurred in the vicinity of Tule Springs where the valley floor attains its greatest width. This shrub is large, in comparison with some of the other desert shrubs, and often attains a height of 3 to 4

feet. The plants were rather widely spaced, averaging 13 per square rod, but the total ground coverage was greater than that of any other community except sagebrush (Table 7).

TABLE 7. Floral composition of 24 quadrat samples taken in the Greasewood Community.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Sarcobatus vermiculatus</i> ... (Hook.) Torr.	100.0	24	4	13.0	100.0	5.6	45.2	29.5	4.4	15.0
<i>Suaeda fruticosa</i> ..... Forsk.	79.2	40	0	10.8	60.0	0	27.2	11.5	0	3.9
<i>Atriplex confertifolia</i> ..... (Torr. & Frém.) S. Wats.	37.5	48	0	2.2	80.0	0	15.8	11.3	0	2.3
<i>Kochia vestita</i> ..... (S. Wats.) Rydb.	20.8	124	0	10.0	74.0	0	9.5	3.2	0	0.3
<i>Distichlis stricta</i> ..... (Torr.) Rydb.	8.3	4 <sup>1</sup>	0	0.3	25.0	0	1.9	9.0	0	0.6
<i>Artemisia spinescens</i> ..... D. C. Eaton	4.2	20	0	0.8	11.1	0	0.4	1.4	0	0.06

<sup>1</sup>Number of patches of sod rather than individual plants of *Distichlis stricta*.

The number of species of plants in this community was very limited in most localities, only 6 occurring in the quadrat samples taken in White Valley. Although salt blites, *Suaeda fruticosa* Forsk., was the principle associate of the greasewood in the vicinity of Tule Springs, the salt bush, *Atriplex nuttallii* S. Wats., was common in some other parts of the valley and *Atriplex falcata* (Jones) Standl. has been reported as a prominent member of this community in other localities (Shantz & Piemeisel 1940). Pickleweed extended into this community from its border around the barren playa as one of the subdominants in the vicinity of Tule Springs. Salt grass formed a solid sod around some of the springs but it did not extend very far out into the greasewoods. Alkali sacton, *Sporobolus airoides* Torr., and big rabbitbrush were only occasionally encountered although in some areas they may be important constituents of this community.

The soil on which this community occurred was usually a heavy clay or clay loam. In some parts of the valley, which are subjected to flooding, the soil surface was hard and baked. In other places

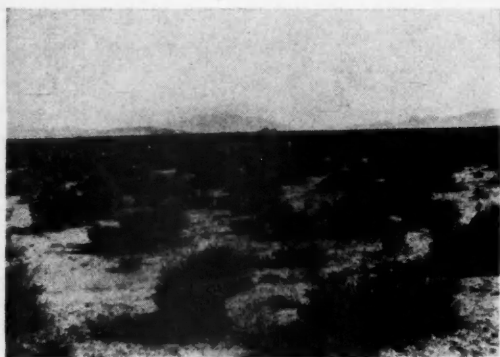


FIG. 11. Greasewood community in White Valley, Millard County, Utah. (Sept. 1, 1940.)



the soil was often so loose that one sank half way to his ankles when walking through it. Some sand dunes were also present thus making a diversity of habitats as far as soil conditions were concerned.

The leaves of the greasewood were later in coming out than those of shadscale and tetradyimia so that during the early spring this community looked very barren in comparison with communities of higher elevations. However, during the summer the picture was completely reversed, the greasewoods became very green and appeared like an oasis in comparison with the tetradyimia community.

The relationship between the greasewood and shadscale communities has been described on page 262, where it was pointed out that a wide ecotone occurs where the two meet in some areas.

*Invertebrates of the shrub layer society*—The greasewoods retained their leaves and remained green throughout the summer and thus maintained a more constant invertebrate population than did some of the other dominant shrubs (Fig. 9).

Spiders were very abundant averaging 4 to 5 specimens per sample (Table 8). In 1939 they were most abundant during the middle part of August when many immatures were present, but during 1940 they were most numerous during the last part of June. *Philodromus* sp., *Dendryphantes* sp., and *Pellenes* sp., were the most abundant and frequently encountered species. The species *Sassacus papenhoei* Peckham occurred less often in quantitative samples than some of the other species but it seemed to be restricted to this community.

Mites occurred much less frequently than in either the shadscale or tetradyimia communities. *Bryobia praetiosa* was most abundant although other species included *Erythraeus* sp. and *Trombidium* sp.

Orthoptera were commonly seen and occurred in the quantitative samples with about the same frequency and abundance as in the tetradyimia community. The nymphs of *Melanoplus* sp. first appeared during early July, becoming most abundant about

July 15. Nymphs of *Aeoloplus t. tenuipennis* were most abundant about August 10.

Hemiptera were far less numerous than they were in the shadscale community and constituted only 6.3 percent of the total invertebrate population. The pentatomids, *Thyanata rugulosa* (Say) and *Chlorochora sayi* Uhl., were more abundant than in any other part of the valley and were most numerous about the middle of August. Miridae was the most abundant family, being represented by 7 species, of which 4 were restricted to this community (Appendix B).

Homoptera constituted half of the total insect population due primarily to the great abundance of one species of membracid, *Echenopa permutata* Van D. This species occurred in 56 percent of the collections and was most abundant during the latter part of July in both 1939 and 1940. The cicada, *Neoplattypedia constricta* Dan's, was conspicuous during midsummer because of its singing and it was an important source of food for some of the lizards of this community. The Cicadellidae were represented by 8 species, of which *Ceratagallia dondia* (Oman) and *Ophiola clavata* (Ball) were the most prevalent. Three species of fulgoroidea were collected of which *Hysterapterum cornutum* Mel. and *Oliarus* sp., were the most numerous. The coccid, *Orthezia* sp., occurred in about 20 percent of the quantitative samples and was most abundant during the early part of May. The greasewood is also the host plant of the aphid, *Aphis bonnevillensis* Knt., although this species was seldom taken in the quantitative samples.

Coleoptera were much more abundant than in the shadscale community. The chrysomelid, *Pachybrachis* sp., was the most abundant species, occurring in almost 50 percent of the collections. The coccinellids, *Hyperaspis fastidiosa* Csy. and *Hippodamia convergens* Guer., were taken in no other community.

Diptera constituted a greater percentage of the total invertebrate population in this community than in any other. They were represented by 19 species of which 10 were taken in no other community (Appendix B.). Agromyzidae was the most abundant and frequently collected family.

The lepidoptera were represented principally by larvae in the quantitative samples. Phalaenidae and Geometridae were the most abundant families and were most common during the middle part of May.

Hymenoptera constituted slightly less than 10 percent of the total invertebrate population. Ants were more abundant on the greasewoods than on any other shrub, the 3 most numerous species being *Tapinoma sessile* (Say), *Formica neogagates* Emery, and *Camponotus* (*Myrmecotoma*) sp. They were most conspicuous during the middle of May.

*The ground layer society*—Tenebrionid beetles were the most conspicuous components of this society and were more numerous than in any other community. Of the following 6 species, *Eleodes hispidaris*, *E. obscura*, *E. hirsuta* Lec., *E. pilosa* Horn, *E. extricata* (Say), and *E. nigrina* Lec., the last 3

TABLE 8. Frequency, average number per square meter (50 sweeps), and percentages of total invertebrates collected in quantitative samples.

Orders	Frequency of occurrence (%)				Average number per collection (M <sup>2</sup> )				Percent of total invertebrates collected			
	Shadscale	Tetradyimia	Greasewood	Sagebrush	Shadscale	Tetradyimia	Greasewood	Sagebrush	Shadscale	Tetradyimia	Greasewood	Sagebrush
Araneida.....	50.0	58.8	70.0	64.7	1.2	1.4	4.6	5.4	8.2	2.4	8.5	6.5
Acarina.....	25.0	35.3	16.1	11.8	3.4	2.5	0.7	0.2	24.2	3.8	1.2	0.2
Collembola.....	3.6	5.9	0	0	0.1	0.3	0	0	0.8	0.4	0	0
Orthoptera.....	14.3	29.4	24.0	35.4	0.2	0.4	0.5	0.8	1.6	0.7	0.9	3.1
Thysanoptera.....	0	11.8	3.2	0	0	10.5	0.1	0	0	15.3	0.1	0
Hemiptera.....	39.3	58.8	54.8	88.2	2.3	37.4	3.0	11.3	16.5	54.0	6.3	13.9
Homoptera.....	57.2	52.9	80.6	64.7	3.4	7.2	27.7	45.1	24.7	10.4	51.1	54.9
Coleoptera.....	32.0	58.8	74.6	82.4	0.7	1.7	4.4	5.5	4.9	2.5	8.1	13.9
Lepidoptera.....	3.6	35.3	32.2	29.4	0.1	0.4	0.5	0.4	0.5	0.8	0.8	0.5
Diptera.....	42.8	52.9	64.5	58.8	1.4	5.0	7.6	1.8	10.1	7.2	14.1	5.8
Hymenoptera.....	35.7	41.2	80.6	47.1	1.1	1.8	4.9	1.6	8.5	2.5	8.9	1.2

were restricted to this community. *Eleodes pilosa* is covered with numerous small hairs to which the white soil of the valley floor adheres thus making it very inconspicuous and easily overlooked. *Eleodes obscura* was not only the most conspicuous tenebrionid because of its size, but it was also the most numerous. It was active both day and night, and was often observed until after midnight. Carrion beetles, *Necrophorus guttulus* Mots. and *N. guttulus hecata* Bland were found wherever an animal had been dead for a day or more. The hisster beetle, *Saprinus* sp., and the dermestid, *Dermestis marmoratus* Say, which also feed on carrion, were usually found in the same carcass with the carrion beetles. So voracious are these beetles that a large jack rabbit would be completely devoured within three or four days.

The hymenoptera were represented primarily by ants of which *Dorymyrmex pyramicus* (Roger), *Solenopsis molesta* (Say), and the harvester ant were the most frequently encountered, the first 2 species being found only on or near sand dunes. The litter beneath the greasewood bushes harbored hymenoptera and assilidae larvae.

#### WINTERFAT COMMUNITY

##### (*Eurotia-Oryzopsis-Microdipodops* Faciation)

Although the shadscale, tetradymia, and greasewood communities were the most extensive and ecologically important communities of the White Valley area there are several others which must also be considered. One of these is the winterfat community, which was probably much more extensive before the advent of white man than it is at the present time. A study of the age of these shrubs in various communities of Pine and Wah Wah Valleys by Stewart, Cottam, and Hutchings (1940), reveals that under conditions of overgrazing winterfat fails to grow and reproduce. Because of its greater palatability it has been greatly reduced in abundance and areas it once occupied have been invaded by the little rabbitbrush.

Winterfat, the principal dominant, has rather high water requirements and is intolerant of high con-



FIG. 12. Winterfat Community in Pine Valley, Milard County, Utah. (Aug. 3, 1940.)

TABLE 9. Floral components of 16 quadrat samples taken in the Winterfat Community.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Eurotia lanata</i> .....	100.0	148	28	106.0	100.0	53.8	83.8	15.7	5.9	8.65
(Pursh) Moq.										
<i>Sphaeralcea</i>										
<i>grossulariifolia</i> .....	50.0	32	0	6.0	21.1	0	4.3	0.8	0	0.2
(Hook. & Arn.) Rydb.										
<i>Atriplex confertifolia</i> .....	25.0	16	0	3.4	30.8	0	5.6	6.3	0	1.1
(Torr. & Frém.) S. Wats.										
<i>Oryzopsis hymenoides</i> .....	25.0	16	0	2.5	20.0	0	2.9	1.8	0	0.23
(Roem. & Shult.) Ricker										
<i>Hilaria jamesii</i> .....	25.0	12	0	2.0	7.1	0	1.2	0.3	0	0.05
(Torr.) Benth.										
<i>Tetradymia glabrata</i> .....	12.5	8	0	1.0	15.4	0	1.9	0.2	0	0.16
A. Gray										
<i>Artemisia spinescens</i> .....	12.5	4	0	0.5	2.2	0	0.3	0.5	0	0.09
D. C. Eaton										

centrations of mineral salts, being found only where the salt content of the soil does not exceed 0.04 to 0.05 percent in the upper 2 feet (Shantz & Piemeisel 1940). It was usually found in the purest stands on a sandy soil which is permeable and which readily absorbs a large share of the available precipitation. It also occurred on sandy soils where water-courses spread out over flat areas and where the normal amount of precipitation is thus augmented by the run-off from higher areas.

This community often occurs as "islands" within the more extensive shadscale community, with which it was always closely associated. These "islands" are readily discernible because of the light color of the dominant plant which may attain a height of 18 inches under most favorable conditions but which is usually only 8-12 inches in height (Fig. 12). Winterfat and Indian rice grass were the principal dominants. The subdominants included galleta grass, globemallow, and bud sage. Gray molly, matchweed, *Gutierrezia sarothrae* (Pursh) Britt., and Rusby, and the little rabbitbrush were also present in varying degrees of abundance under conditions of overgrazing. *Astragalus cibarius* Sheld., *Eriogonum cernuum* Nutt., *E. hookeri* S. Wats., and *Sphaerostigma boothii* (Dougl.) Walp. also occur in this community in Escalante Valley (Shantz & Piemeisel 1940).

#### BLACK SAGE COMMUNITY

##### (*Artemisia nova-Atriplex-Neotoma* Faciation)

Situated along the west border of the White Valley floor, near the central and north-central parts of the valley, are several black lava rock knolls which attain an elevation of slightly over 5,000 feet above sea level (Fig. 13). The soil on these knolls is very shallow. Large rocks and cliffs comprise a large part of the terrain.

Black sage, *Artemisia nova* A. Nels., was the most prevalent dominant. Other dominants included shadscale, at the lower elevations of the community, and 2 species of tetradymia, *Tetradymia spinosa* Hook. & Arn. and *T. glabrata* A. Gray, at the higher elevations. Galleta grass and wheat grasses, *Agropyron* spp., were conspicuous among the dominant shrubs.

TABLE 10. Floral components of 24 quadrat samples taken in Black Sage Community.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Artemisia nova</i> .....	83.3	20	0	9.2	62.5	0	22.5	7.8	0	3.4
A. Nels.										
<i>Chrysothamnus stenophyllus</i> .....	83.3	64	0	13.2	66.7	0	20.3	6.4	0	1.5
(A. Gray) Greene										
<i>Hilaria jamesii</i> .....	75.0	80	0	19.2	71.5	0	23.2	10.4	0	2.0
(Torr.) Benth.										
<i>Tetradymia spinosa</i> .....	41.7	12	0	3.0	33.3	0	6.9	8.3	0	2.3
Hook. & Arn.										
<i>Atriplex confertifolia</i> .....	33.3	96	0	9.6	63.1	0	8.4	8.8	0	0.9
(Torr. & Frém.) S. Wats.										
<i>Agropyron</i> spp.....	25.0	20	0	2.7	17.8	0	2.9	1.6	0	0.4
<i>Ephedra</i> spp.....	25.0	8	0	1.6	14.3	0	2.5	4.0	0	0.8
<i>Suaeda fruticosa</i> .....	16.7	56	0	7.0	43.7	0	6.7	1.5	0	0.2
Forsk.										
<i>Oryzopsis hymenoides</i> .....	16.7	4	0	0.7	16.7	0	2.0	0.7	0	0.07
(Roem. & Shult.) Ricker										
<i>Tetradymia glabrata</i> .....	8.3	12	0	1.0	33.3	0	2.8	8.8	0	0.7
A. Gray										
<i>Artemisia spinescens</i> .....	8.3	8	0	0.6	12.5	0	1.0	0.3	0	0.03
D. C. Eaton										
<i>Eurotia lanata</i> .....	8.3		0	0.3	8.3	0	0.8	0.3	0	0.03
(Pursh) Moq.										

The jointfir, *Ephedra viridis* Coville, was scattered throughout the community being most abundant at higher elevations. *Lophamia stansburyi* A. Gray occurred in the more rocky situations, being especially conspicuous along crevices on the face of cliffs. Other floral components included Indian ricegrass, three-awn grass, little rabbitbrush, gray molly, and matweed.

The invertebrates of this community were not investigated but the minor influent animals were found to be very distinct.



FIG. 13. Shadscale community in foreground and Black Knolls on which the black sage community occurred in White Valley, Millard County, Utah. (July 2, 1940.)

#### PICKLEWEED COMMUNITY

This community (Fig. 10) forms a narrow fringe around the barren playa adjacent to the greasewood community in the vicinity of Tule Springs. The dominant plant, *Allenrolfea occidentalis* (S. Wats.) Kuntze, is highly salt-tolerant and is largely restricted to areas where the salt concentration is beyond the tolerance of the greasewoods. Consequently

TABLE 11. Floral components of 8 quadrat samples taken at the convergence of the Greasewood and Pickleweed Communities.

Species	Frequency	Abundance			Composition			Coverage		
		Max.	Min.	Ave.	Max.	Min.	Ave.	Max.	Min.	Ave.
<i>Allenrolfea occidentalis</i> .....	100.0	76	4	41.6	100	50	91.6	13.5	6.2	9.0
(S. Wats.) Kuntze										
<i>Sarcobatus vermiculatus</i> .....	37.5	4	0	1.5	50	0	8.4	6.7	0	2.4
(Hook.) Torr.										

it is seldom accompanied by any other plants. The greasewoods which do occur in this community were usually stunted, yellowish in color and very sickly looking.

#### THE LITTLE RABBITBRUSH ASSOCIES<sup>8</sup>

The most common species of little rabbitbrush was *Chrysothamnus stenophyllus* (A. Gray) Greene; however, in certain localities this species may be accompanied by several other species including *C. laricinus* Greene, *C. puberulus* (D. C. Eaton) Greene, and *C. Greenei* (A. Gray) Greene, all of which are very similar in general appearance and cannot be reliably distinguished in the field. Their ecological requirements also seem to be apparently the same so that these offer no criteria for differentiating them. The landscape aspect of this community is very distinct, especially where it is adjacent to the winterfat community which is much lighter in color (Fig. 14).

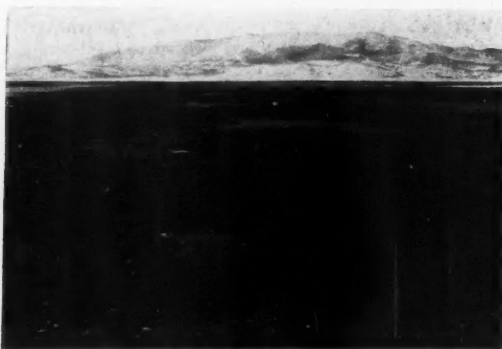


FIG. 14. Little rabbitbrush community (dark vegetation) within which are interspersed "islands" of winterfat (light vegetation) in Antelope Valley, Millard County, Utah. (Aug. 9, 1940.)

This community is not found on soils with a high mineral content or on heavy soils where the water table is near the surface. It was most abundant where a hard-pan is near the surface or on sandy or rocky soils where there was little or no competition with the climax dominants of the area. It quickly invades areas where winterfat and shadscale have been removed or reduced in vitality and abundance.

<sup>8</sup> An associates is the developmental stage of the climax community (association). It is characterized by its lack of permanence and is replaced by another community in the process of development or succession.

Because it is less palatable than some of the dominant shrubs it suffers less from the effects of grazing and consequently occupies a greater area at the present time than it did before man's domestic animals were introduced. There is a high negative correlation between little rabbitbrush and winterfat and Indian ricegrass and when the winterfat and ricegrass are decreased in abundance the little rabbitbrush is greatly increased (Stewart, Cottam & Hutchings 1940).

## THE SAGEBRUSH COMMUNITY

### EXTENT AND CLIMAX STATUS

The sagebrush community (*Artemisia-Agropyron-Lepus* Association) is one of the most important biotic communities of the Northern Desert Shrub Biome. It was formerly very widespread throughout the northern Great Basin area and the Columbia River Drainage Basin, but has been greatly reduced by the agricultural pursuits of man. Scattered fragments extend as far south as the Mexican border, but it ceases to be a dominant about 70 miles south of Modena, Utah where it merges into the Southern Desert Scrub Biome. Within the piñon-juniper association it often forms a shrub layer beneath and between the dominant trees, and it may extend to elevations of 8,500 feet as a scattered remnant in the open areas within the lodgepole pine association (Svihla 1932).

The northern limit of this association merges into the grassland communities of northern Utah, southern Idaho and southeastern Washington. As has been pointed out by Weaver (1917) no sharp geographical line can be drawn where these two biomes meet. The moisture requirements for the driest grassland community (*Agropyron* Association) and the sagebrush community are very similar, the principal difference being in the distribution of the precipitation during the year (Fig. 2). The similarity in the climatic requirements of these two communities is reflected in the compatibility of the dominants, *Agropyron spicatum* (Pursh) Scribn. & Smith, the principal dominant of the *Agropyron* community, together with other associated grasses and herbs such as *Stipa commata* Trin. & Rupr. and *Balsamorhiza sagittata* (Pursh) Nutt., occur as common associates of the big sagebrush within the *Artemisia* community. Thus it is often difficult to determine just what the true climatic climax community is within this ecotone area where the two biomes converge, and it is possible that various disturbances, such as over-grazing and fire, may be largely responsible for determining the relative abundance and dominance of one or the other of the principal dominants at the present time.

There is considerable evidence in certain areas of Utah (Pickford 1932 and Stoddart 1941), southern Idaho (Craddock and Forsling 1938), Idaho and Washington (Humphrey 1945), that over-grazing decreases or eliminates the competition of the more palatable dominant grasses and promotes the de-

velopment of a disclimax sagebrush community. Within these same areas it is evident that sagebrush is greatly reduced when burned and may be practically eliminated by fire in the drier areas (Pickford 1932, Daubenmire 1942). To what extent fire may have destroyed large areas of climax sagebrush, even before the advent of white man is problematical. Captain Bonneville, whose early explorations date back to 1832, made note of the fact that the sky was darkened for days at a time by smoke from fires that were set by the Indians (Irving 1843). Much of the evidence used to support the theory that many of the present sagebrush areas are disclimax is based on observations of unplowed corners of cultivated fields, roadways, cemeteries, etc. The degree to which such areas have been protected from grazing is usually quite certain but the history of such areas as to the previous occurrence of fires is not always known. Many of the areas used as cemeteries have originally been burned and the remaining stubs of sagebrush removed.

The dominance of sagebrush and its ability to resist the artificial establishment of forage grasses, in the vicinity of Wells, Nevada, is attested by Robertson (1943) who reports that for the successful establishment of grass seedlings, the vigor and competition of the sagebrush for soil moisture must be reduced by pruning its roots with a scarifier or ripper to a depth of 9 to 12 inches below the soil surface.

The evident dominance of sagebrush in Idaho has been determined by Egger (1941) who studied the succession of plant communities on the volcanic deposits of the Snake River plains area and found that the primary communities are all replaced by a climatic climax association dominated by six shrubs, of which *Artemisia tridentata* is the principal one, and five important grasses. It is his opinion that, "Sage is and evidently has been a dominant member of the vegetation since the advent of white man into the region." (Egger 1941, p. 280).

### BIOTIC MATRIX

*Dominants and subdominants*—Sagebrush communities are largely confined to deep, permeable, salt-free soils of well-drained valleys and bases of mountain ranges, especially alluvial fans. The soils vary in texture from clay and sandy loam to gravel and usually have a high water-holding capacity. Big sagebrush, the principal dominant, has a long tap root with numerous lateral branches which facilitate its utilization of moisture to a considerable depth as well as near the surface of the soil. Where sufficient soil moisture is available at depths of 3 to 6 feet and where the salt content of the soil is very low this plant attains its greatest growth, becoming 4 to 6 feet in height and having a trunk diameter of 5 inches or more (Fig. 15). In areas where there is a hard-pan within 12 to 18 inches of the surface or where the salt content of the soil becomes more than 0.5 percent in the third or fourth foot it fails to thrive and becomes sickly looking (Kearney, Briggs, Shantz, et al. 1914).



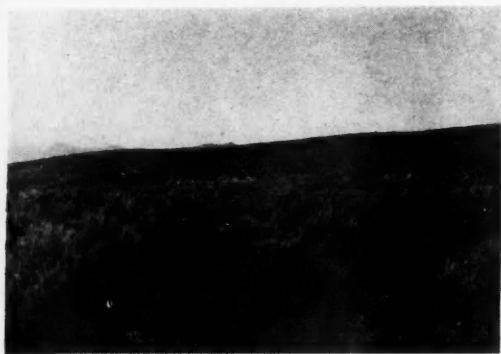


FIG. 15. Sagebrush community in Fernow Valley, Juab County, Utah. (Aug. 3, 1939.)

Sagebrush may occasionally be found associated with the more salt-tolerant shrubs such as shadscale and greasewood but when it does extend into these other communities it is found only along ravines where the soil is deeper, more permeable and well drained. On rocky knolls and hillsides, where the soil is more shallow and coarser in texture, the big sagebrush is replaced by black sage, *Artemisia nova* A. Nels.

When sagebrush is removed by burning or cultivation, various annual and biennial subdominants such as brome grass, *Bromus tectorum* L., Russian-thistle, pigweeds, *Amaranthus* spp., sunflower, *Helianthus annuus* L., and verbena, *Verbena bracteosa* Michx., invade and occupy the area. Such plants are usually replaced by matchweed which eventually gives way to the dominant sagebrush and its associates under natural conditions.

Sagebrush forms one of the most dense covers of any of the shrubs encountered. The individual bushes grow much closer together and in some places in Fernow Valley attain almost treelike proportions. Unfortunately Fernow Valley is a winter range for sheep and consequently much of the virgin herbaceous undergrowth has been removed. However, remnants of the following dominant grasses still persist: wheat grass, *Agropyron spicatum* (Pursh) Scribn. & Smith, needle-and-thread grass, *Stipa comata* Trin. & Rupr., Indian rice grass, and galleta grass. Other herbaceous components include the three-awn grass, *Aristida longiseta* Steud., squirrel-tail grass, brome grass, balsam root, *Balsamorhiza sagittata* (Pursh) Nutt., sego lily, *Calochortus nuttallii* Torr. & Gray, plantago, *Plantago purshii* Roem., and Shult., phlox, *Phlox* sp., milk-vetches, *Astragalus Uintahensis* Jones and *A. cibarius* Sheld., *Applopappus nanus* (Nutt.) D. C. Eaton, *Eriogonum cernuum* Tenue Torr. & Gray, *Erigeron pumilus* Nutt., *Castilleja* sp., and *Crepis occidentalis* Nutt. These plants were not sufficiently numerous nor large enough to alter the aspect of the community but they formed an integral part of the biotic matrix during the spring and summer. Big rabbitbrush

was prevalent along ravines at the lower end of the valley. *Atriplex nuttallii* and Russian-thistle were abundant within small areas in the central part of the valley which had been previously cultivated.

*Invertebrates of the shrub layer society*—The invertebrate population was about the same as in the greasewood community, reaching a maximum during June (Fig. 9). The late summer decline was less rapid than in the shadscale and tetradychia communities where the dominant plants were more widely spaced and where there was a considerable amount of defoliation due to the more xeric conditions to which those communities are subjected.

Spiders were very prevalent and averaged 5.4 per collection. Most species became most abundant during the latter part of July and early August when a great many immatures were present. The most abundant species were *Philodromus* sp. and *Dendryphantus* sp. Species collected in no other community included *Xysticus concolor* Thorell and *Leius* sp.

*Atomus arvensis* Bks. was the only species of mite collected and it occurred with a frequency of only 11.8 percent (Table 8).

Grasshoppers were taken in about one-third of the quantitative sweepings but constituted only 3.1 percent of the total invertebrate population although they were very frequently seen.

The hemiptera were very distinct. Seven of the 15 species collected were found in no other community. They occurred in almost 90 percent of the collections and constituted about 14 percent of the total invertebrate population (Table 8). Miridae was the most prevalent family and *Chlamydatus uniformis* Uhl. and *Tuponia* sp. were the most numerous species. The wide-ranging damsel bug, *Nabis alternatus* Parshley, occurred with greater frequency in this community than in any other. The greatest total abundance of hemiptera occurred during June but a few species were most numerous during the latter part of the summer.

Homoptera were more prevalent in this community than in any other. They averaged 45.1 individuals per collection and constituted 54.9 percent of the total invertebrates collected. The spittle bug, *Clasoptera brunnea* Ball, occurred in 35.3 percent of the collections and was taken in no other community. Cicadas, *Neoplattypedia constricta* Dan's, were very conspicuous although they were seldom taken in quantitative collections. They tend to remain close to the main branches of the sagebrush and thus escape being taken when sweepings are made. Cicadellids were far more numerous than in any other community, the most prevalent species being *Empoasca nigra typhlocyboides* G. & B., *E. sp. (nigra group)*, and *E. sp. (aspera group)*. The fulgorid, *Hysteropterum cornutum* Mel., was more abundant in this community than in any other and occurred in 52 percent of the quantitative collections.

Coleoptera averaged 5.5 per collection and constituted almost 14 percent of the total invertebrate population (Table 8). Coccinellids were abundant

and very distinct. Six species were collected, none of which occurred in any other community. The most abundant of these were *Hippodamia apicalis* Csy., *Scymnus* sp., and *Hyperaspis lateralis montanica* Csy. The most abundant chrysomelid was *Pachybrachis* sp., but it was less abundant than in the greasewood community. Two species of snout beetles, *Promecotarus densus* Csy. and *Apion sordidum* Smith, were fairly common and were not encountered elsewhere.

Lepidoptera constituted less than 1 percent of the total invertebrate population. Only 6 larvae representing 3 families were collected in all the quantitative samples.

Although diptera occurred in more than 50 percent of the collections they were never abundant and made up only 5.8 percent of the total invertebrates collected. Bombyliids belonging to the genus *Geron* were the most common.

Hymenoptera were also scarce, only 6 species of ants and 4 species of parasitic hymenoptera were collected (Appendix B). The ants most frequently taken were *Camponotus* (*Myrmentoma*) sp., *Monomorium minimum* (Buckley), and *Iridomyrmex* sp.

**Ground layer society**—The most conspicuous component of this society was the western harvester ant which was far more abundant than in any other community. The number of its mounds varied from 4 to 8 per acre with an average of 6.2 for five 1-acre plots. The effect of these ants on the vegetation adjacent to their mounds was very striking. Around each mound all the vegetation was removed for a distance varying from 2.5 to 12 feet. Thus the denuded area per mound varied from 95 to 454.4 square feet with an average of 300.7. Their coactions within the community not only involved the plants which they feed on and store in their burrows but they were also observed carrying insects into their mounds. Another ant which was not so frequently encountered because it is nocturnal was *Camponotus maculatus vicinus* Mayr. This is a large brown ant whose burrows were found to extend two to three feet below the surface of the ground, usually at the base of a large sagebrush. This species is carnivorous and often stripped almost all the skin and flesh from the heads of trapped rodents.

Although grasshoppers were seldom taken in the quantitative sweepings from the sagebrush, they were very common both on the vegetation and on the ground. The 2 most numerous species were *Trimerotropis p. pallidipennis* (Burm.) and *Trimerotropis g. gracilis* (Thomas).

Two beetles encountered only in this community included the carabid, *Pterostichus californicus* (Dej.), and the cerambycid, *Prionus palparis* Say. Tenebrionid beetles were far less abundant than in other communities, *Eleodes obscura* (Say) being the only species collected.

## INFLUENT ANIMALS

### MAJOR PERMEANT INFLUENT<sup>9</sup>

#### Mammals

The badger, *Taxidea taxus* ssp., has been greatly reduced by the predator control practices intended for the coyote (Davis 1939, Hall 1930, Dixon 1930, and Howell 1930), but it is still present throughout all the communities studied. Its presence is conspicuously revealed by the excavations it produces in search of ground squirrels, kangaroo rats, and pocket gophers. Fresh diggings were found in every community except winterfat, however, old excavations being utilized by burrowing owls, were also found in that community. For some reason the number of excavations found in 1940 were much fewer than the number in 1939. Inasmuch as the ground squirrels were much less numerous in 1940 than in 1939, it may be possible that the badgers had gone to other areas in search of these prey. The Tule Springs area, where ground squirrels were abundant, was visited both years by badgers, and near cultivated areas of Desert and Garrison, where ground squirrels were prevalent both years, badger excavations were very much in evidence.

The excavations produced by the badger are utilized to a great extent as dens and places of refuge by many other animals. The burrowing owl is almost entirely dependent on the badger for providing it a place of abode. Coyotes often enlarge badger holes and use them as dens in rearing their young. They were used to a very great extent by cottontail rabbits both as a place of refuge when being pursued and also as a place in which to rear their young. Rodents often use them as retreats and as permanent places of residence. Lizards and snakes retreat into them in times of danger and to hibernate. Rock wrens were using abandoned badger holes as a nesting place in the tetradyemia community.

The kit fox, *Vulpes macrotis* ssp., ranges throughout the biome but it has been considerably reduced in numbers by trapping and poisoning campaigns. Yarrow (1875, p. 55), in referring to this species says, "It is thought to be tolerably common in Utah and Nevada, as Indians were seen with skins in their possession." Four dens of this species were found, one of which was located in the winterfat area and the others in the shadscale. The dens were located in open areas unprotected by vegetation, but since the kit fox is largely nocturnal and remains in its den during most of the day, protective vegetative cover is not so important as in the case of the coyote. When it does come out during the day it ventures only a short distance from its den and depends very largely on the den as a means of escape.

The kit fox is small and feeds on smaller prey than does the coyote. Around the mouth of two of the dens were strewn the remains of many rodents

<sup>9</sup> "Major influents" is an arbitrary category which includes the larger mammals and birds whose coactive effects within the community are significant, primarily because of their size. The term "major" is not used in the sense that members of this category are biotically of major (greatest) importance within the community.

on which these foxes had been feeding. Among these were 19 kangaroo rats, 2 kangaroo mice, 1 pocket mouse, 1 white-footed mouse and rabbit bones. So important is the kangaroo rat in the diet of this fox that in some areas its distribution is found to be very closely correlated with that of the kangaroo rat (Bailey 1931).

The coyote, *Canis latrans lestes* Merriam, is one of the most important major influents of the biome. Although it was more abundant in some communities than others it ranged throughout all of them. No quantitative data were obtained as to the absolute abundance of this species, but signs such as tracks, scat, dens, and calls indicated that it is much more abundant in the greasewood and sagebrush communities than in the more open type of communities.

Three dens were located in the greasewood community but only one was in use at the time they were found. The active one was located almost in the center of White Valley near the south end and looked as if it had originally been a badger excavation that had been cleaned out and enlarged by the coyote. The burrow was in the east side of a greasewood-covered hummock and sloped slightly downward at its entrance but was practically horizontal the remainder of the way back. The evening it was found the young whelps could be plainly heard not far back from the entrance. When the den was visited the following day all the whelps had been removed. This demonstrates how cunning these animals are, a factor which has undoubtedly been responsible for their perpetuation in spite of the heavy pressure constantly being exerted to exterminate them.

Coyotes breed from late January to early March in Utah and Nevada, and the whelps are usually born in April and early May (Hamlett 1938). The size of the litter may vary from 4 to 17 with 7 being about the average number produced. Two litters which were dug out in White Valley in 1940 by Civilian Conservation Corps workers each consisted of 6 whelps. When the young whelps are 8 to 10 weeks old the family leaves the den and travels together for a considerable time (Young & Dobyns 1937). Young coyotes about half to two-thirds grown were not seen alone until August.

The coyote is a very important coactor within all the communities because it is active throughout the year and because of the large number of biotic components which it utilizes as food. Its food habits have been studied very extensively because of its economic importance (Lantz 1905; O. J. Murie 1935; A. Murie 1940; Sperry 1933, 1934, 1939, 1941; Bond 1939). These studies indicate that rabbits are the coyote's main source of food. Practically all types of rodents are also included in its diet as well as birds, reptiles, insects, and some vegetable matter. Rabbits occurred in 43 percent of the 8,339 coyote stomachs examined by Sperry (1941), and ranged from 37 percent in September to 52 percent in May; they constituted 33.25 percent of the total food volume. Rabbits and rodents together constituted more than 50 percent of the food eaten. One stom-

ach from a female coyote collected in California contained 30 pocket mice and one kangaroo rat. Reptiles occurred in 3 percent of the stomachs examined by Sperry and snakes occurred about two and a half times as often as lizards. The number of insects eaten by coyotes is usually small but in some cases the total stomach contents have been found to be composed of insects (Sperry 1941). Murie (1940) observed coyotes feeding on grasshoppers on several occasions.

Although a continuous warfare is waged against the coyote by stockmen and the Predator and Rodent Control Division of the Fish and Wildlife Service it continues to be very abundant. From July 1, 1915 to June 30, 1939 the Fish and Wildlife Service agents killed a total of 86,889 coyotes in Utah, or an average of 3,620 per year. During the fiscal year of 1939 from July 1 to June 30, 1940, 19,513 coyotes were killed. The average yearly kill from 1915 to 1940 amounted to 4,056. A large portion of these were taken in western Utah because that part of the state is the principal winter range of sheep and is consequently the focal point of predator control activities. In Millard County alone, 6,465 coyotes were killed by the Fish and Wildlife Service from 1930 to March 1941, although no regular campaigns were conducted during 1935 and 1936. The numbers killed per year varied from 53 in 1930 to 1,188 in 1940 (Zimmerman, personal correspondence). These numbers do not include the ones that were not found after being poisoned or the ones that were killed by stockmen and individual trappers not in the employ of the government. This increase in the yearly number killed may be due to an increase in the number of government predator control agents in the field and the development of more efficient trapping and poisoning methods and does not necessarily mean that coyotes are increasing in numbers. However, many long-time resident stockmen in western Utah are of the opinion that coyotes are just as abundant now as they have ever been within their experience. The elimination of part of the coyote population decreases the competition for food of those that remain and thus increases the survival value of themselves and their offspring. Since much of the predator control work is done during late summer, autumn, and winter most of the survivors of these seasonal campaigns are able to reproduce the following spring and bring forth a new generation to replace the ones that were killed the previous year. The cunningness of the coyote has enabled enough of them to survive each winter so that there is an ample breeding stock each spring to restock the area again by autumn.

Evidence of the bobcat, *Lynx rufus* ssp., was found only twice. The tracks of one were found along a dusty road in the shade about 3 miles below the base of the mountains and one was seen in King Canyon on the west side of White Valley May 21, 1940. This species is probably only an occasional visitor in these valley communities and is of very little ecological importance.

Remnants of the once-numerous pronghorned ante-

lope, *Antilocapra a. americana* (Ord), still remain within the Great Basin. Their numbers are greatly reduced at the present time but the small scattered bands that still exist indicate that they originally ranged throughout Utah and Nevada. In 1922-24 the total number of antelope in Utah was estimated to be 670, of which 520 occurred in the western part of the state (Nelson 1925).

At the present time the antelope is given full protection and in some places is showing signs of increasing. Fourteen head were seen in the area between White Valley and Pine Valley during the two summers that were spent in that area, 5 being the maximum number seen at any one time. Groups of 16 to 20 were observed by local residents in the north end of White Valley and in the vicinity of the Desert Range Experiment Station during the winter of 1939-40. A Fish and Wildlife Service trapper reported a band of about 20 head in the vicinity of Fish Springs just north of White Valley during the summer of 1940. During the summer the antelope tend to scatter out and remain in the low hills and are consequently seldom seen in the valleys. Reports of sheepherders and Civilian Conservation Corp workers indicate that during the winter they congregate in much larger bands and are more commonly seen in the valleys.

Although the antelope reached its greatest abundance in the short grassland communities of the western plains region it was never restricted to such areas. Evidence from the early explorers of Utah and Nevada and testimonies of early residents make it very certain that the Great Basin supported thousands of these animals before white man began taking his toll. Although grasses may be very important in the diet of this animal it also consumes a large amount of browse from shrubs, especially in winter (Rouse 1941).

The antelope is not restricted to any one community but ranges throughout all of them. Although the reduced numbers now present probably exert very little influence in the communities as a whole their browsing and grazing effects on the vegetation may be noticeable where larger bands of these animals occur. Under natural conditions they constituted a basic part of the food supply of such predators as the coyote and bobcat, especially during the winter when the snow would tend to impede their movements. Nelson (1922, 1923) reported that a herd of 60 antelopes, at the National Bison Range, Montana, were destroyed by wildlife predators (chiefly coyotes) and Indian dogs during the winters of 1921-22 and 1922-23.

#### Birds

The major influent birds observed include the Cooper hawk, *Accipiter cooperii* (Bonaparte), western red-tailed hawk, *Buteo jamaicensis calurus* Cassin, Swainson hawk, *Buteo swainsoni* Bonaparte, golden eagle, *Aquila chrysaetos canadensis* (Linnaeus), Southern bald eagle, *Haliaeetus l. leucoc*

*phalus* (Linnaeus), marsh hawk, *Circus cyaneus hudsonius* (Linnaeus), prairie falcon, *Falco mexicanus* Schlegel, western burrowing owl, *Speotyto cunicularia hypugaea* (Bonaparte), and the long-eared owl, *Asio otus wilsonianus* (Lesson).

The Cooper hawk and red-tailed hawk were seen only occasionally during late summer and were of little ecological importance within these communities because of their limited numbers and limited seasonal activities.

The Swainson hawk ranged throughout all the communities and was seen throughout the summer, being most common in the sagebrush areas. Two nests were located April 11, 1940 in juniper trees adjacent to Fernow Valley. These hawks were most frequently seen foraging for food about 8 to 10 o'clock in the morning and about 5 o'clock in the afternoon. Animal remains at their nests indicate that they feed on insects, chiefly grasshoppers, as well as chipmunks and ground squirrels.

The biotic influence of eagles is very small, being practically negligible in the case of the bald eagle. Only two individuals of this species were seen during the entire period of investigation. The golden eagle was seen more frequently but it was not common. Rabbits seem to be the principal source of food of this species. On 3 occasions golden eagles were flushed from the greasewood community where they were feeding on freshly killed jack rabbits.

Marsh hawks were consistently seen only in the greasewood community and near cultivated areas in the vicinity of Deseret, Hinkley and Garrison, but they were occasionally seen foraging over practically all communities. Either one or the other of a pair was regularly seen in the vicinity of Tule Springs but no nest could be located. On several occasions these hawks were observed catching lizards. Since diurnal species of rodents are scarce in these communities it is possible that lizards may be a very important source of food for the marsh hawk in such areas. Linsdale (1938), reports that during 6 weeks of observation in Nevada, lizards were brought to the nests of this hawk more often than any other kind of food. He (Linsdale 1936a) also makes reference to the fact that stomachs of the marsh hawk, taken at Pyramid Lake in Nevada by Ridgway, contained nothing but small lizards.

The prairie falcon is a fairly common summer resident in White Valley. It was seen with a frequency of 35 percent in 1939 and 28 percent in 1940. This species is widely distributed and ranges throughout all the biotic communities. Although it nests in the low cliffs of the adjacent mountains it does much of its foraging within the valley communities. One nest was found on a shelf beneath an over-hanging ledge about 30 feet above the base of a perpendicular cliff. Small birds are probably preyed upon to a greater extent by this hawk than by any other, and lizards are also an important item in its diet from the evidence at the nest previously mentioned. These hawks were observed in pursuit of passerine birds on several occasions and their pres-



ence would always cause considerable alarm among the smaller birds. Rodents are also preyed upon by this species (Fisher 1907, Dawson 1923, Tyler 1923), as well as rabbits (Henninger & Jones 1909, Decker & Bowles 1930), and lizards and insects (Fisher 1893, Traverer 1934).

The burrowing owl occurred in all communities except sagebrush and was most abundant in the more open shadscale areas where the vegetation was sparse. In all instances except one it was occupying badger burrows. No colonies or aggregations were found such as have been described by Dawson (1923), but the pairs or family groups occurred by themselves. The shortest distance between any two pairs was 362 meters and in most cases they were from one-fourth to more than a mile apart.

The time of their egg-laying and hatching was not determined but the young were seen around the entrance of the burrows and able to fly during the middle part of July. Seven was the maximum number found in any one family, the size of the family usually ranging from 3 to 5.

This species is diurnal as well as nocturnal and was found outside its burrow at all times of the day. They were never observed hunting during the day but were seen flying about at night. The abundance of nocturnal animals utilized by them as food also indicates that they do a large part of their feeding at night. An examination of regurgitated pellets and animal remains about the entrance of their burrows indicate that their basic source of food is kangaroo rats and insects. Kangaroo rat remains were found in 100 percent of the pellets examined and insects in 96 percent. The insects eaten included grasshoppers, sand crickets, tenebrionids, and scarabaeids, together with scorpions. Other prey included pocket mice and white-footed mice as well as an occasional lizard.

The effect of this owl on rodent populations was very pronounced. A maximum of 3 rodents were caught in 4 nights on two 0.2-hectare and one 0.4-hectare plots where families of these owls were located. Other plots of equal size produced from 5 to 48 rodents during 4 nights' trapping where no owls were present. To what distance around their burrow the owls keep the rodent population at such a low ebb was not determined but it must be much greater than the boundary of a 0.4-hectare plot because other trapping data indicate that kangaroo rats travel several hundred yards away from their burrows. Had they not been depleted within that distance from the burrow more of them should have wandered into the area and been taken in the traps.

The long-eared owl was encountered in the black sage community in White Valley and the sagebrush community in Fernow Valley. One individual was consistently flushed from a ravine near the top of the Black Knolls. This species is usually found in the vicinity of tall shrubs or trees and the writer was very much surprised to find it within this area. As many as 3 individuals were seen along a deep ravine in Fernow Valley.

#### MINOR INFLUENTS<sup>10</sup>

##### Mammals

Bats were only periodically seen except at the Desert Range Experiment Station where a group of 5 desert pallid bats, *Antrozous p. pallidus* (LeConte), occupied the gable end of a building which they used as a place from which to hang while they consumed their food. The remains of 43 scorpions and 17 sand crickets were strewn along a window ledge below the bats over a period of three nights. The heads of some of the sand crickets would still be alive the next morning after the bats had consumed most of the other parts of their bodies. These are both terrestrial invertebrates and their capture would necessarily require that the bats go to the ground to get them. Although feeding on terrestrial non-flying invertebrates is rather unusual for most bats, it is apparently a common practice in this species, (Grinnell 1918, Nelson 1918, Hatt 1923, Huey 1936). These reports also list mole crickets, grasshoppers, and beetles as being taken by the pallid bat.

Other species of bats include the black-nosed bat, *Myotis subulatus melanorhinus* (Merriam), the pallid big brown bat, *Eptesicus fuscus pallidus* Young, and the Mexican free-tailed bat, *Tadarida mexicana* (Saussure).

Weasels were rarely seen but their apparent scarcity may be due to their secretive and nocturnal activity. One Nevada long-tailed weasel, *Mustela frenata nevadensis* Hall, was found on the highway about seven miles west of Hinekey and one other specimen was seen in a ground squirrel burrow within the greasewood community. They were reported as being seen only rarely at the Desert Range Experiment Station.

No evidence of the striped skunk, *Mephitis major* ssp., was found during the study of these communities. The writer suspected that it might occur in White Valley in the vicinity of Tule Springs but no evidence of its presence could be found. It is reported to be common near springs on Antelope Island in the Great Salt Lake (Marshall 1940).

The little spotted skunk, *Spilogale gracilis saxatilis* Merriam, occurred in rocky areas near the mouths of canyons just above the border of White Valley. A family was also found beneath an old building at the Desert Range Experiment Station. Because of their limited distribution these mammals are of little ecological importance in the communities studied but they may be important in other parts of the Great Basin where they are more abundant because of their food habits. Insects, chiefly grasshoppers and beetles as well as mice, rats, small birds, and lizards, are preyed upon by this skunk (Howell 1906).

The piute ground squirrel, *Citellus townsendi mollis* (Kennicott), is widespread throughout Utah

<sup>10</sup> The term "minor influents" is not used in the sense that members of this group are biotically less important than the major influents, but it is used as an arbitrary category which includes those smaller mammals, birds and reptiles which occur within the community. In many cases, members of this category may be biotically more important than some of the major influents.

and Nevada and becomes very numerous in some areas. These rodents tend to occur in colonies so that their distribution is usually spotty and localized. These concentrations were found where there was the greatest abundance of green herbaceous vegetation and consequently this species was most numerous near cultivated fields and in grassy areas around springs. They were only occasionally seen in the sagebrush community at Fernow Valley but were common in sagebrush areas farther south in the vicinity of Fillmore and Beaver, Utah. Very few were encountered in the shadscale, tetradymia and winterfat communities of White Valley, but they were numerous in the greasewood community in the vicinity of Tule Springs where there was an ample supply of salt grass.

They come out of hibernation during late February and early March, and according to Alcorn (1940), the males appear about two weeks before the females. Their breeding season must occur very soon after they come out of hibernation because by May 5, the young had emerged from their burrows and were actively feeding. Their seasonal activity is of short duration because they begin to aestivate during late summer. The time of aestivation seems to be correlated with the availability of food materials and the accumulation of body fat (Alcorn 1940). Consequently the males go into aestivation first and the young last. By the middle of June the adults had begun to aestivate and by the first of August none could be found in White Valley although young were seen as late as August 4 at higher elevations of the Confusion Range.

During their short seasonal period of activity they spend much of their time outside their burrows, voraciously feeding (Table 12). Grasses and other herbaceous plants seemed to be the principal source of their food but greasewoods are also utilized. The young ground squirrels often climbed to the tops of the greasewood where they fed on the terminal buds. They are not strictly herbivorous because they were observed feeding on individuals of their own species which had been killed by passing automobiles.

Their diurnal activities expose them to considerable predation by hawks and snakes. The stomach contents of two rattlesnakes and one gopher snake all contained ground squirrels. One of the rattlers had swallowed two young about two-thirds grown. They are also a favorite source of food for badgers. A badger began working on the colony at Tule Springs May 29th and within a week it had dug out 23 burrows.

The antelope ground squirrel, *Citellus l. leucurus* (Merriam), was very common during the summer of 1939 and was observed in all the biotic communities. At the writer's base camp these animals were so abundant that special precautions were necessary to keep them from robbing the tent. They were most abundant in the shadscale and tetradymia communities. They were seldom seen in the greasewood and seem to prefer the higher elevations where the vegetation is more sparse. Only 2 were caught in the

TABLE 12. Counts of the Piute ground squirrel in an area 15 meters wide and 72 meters long (0.37 acre), at Tule Springs, White Valley.

May 5, 1940					May 17, 1940				
Time of day	Temp. °F	No. of Squirrels			Time of day	Temp. °F	No. of Squirrels		
		Adults	Young				Adults	Young	
5:00 a.m.	45	0	0		6:00 a.m.	55	3	0	
5:30	46	2	0		6:15	57	3	5	
6:00	48	4	2		6:30	58	2	4	
6:15	48	3	2		6:45	58	4	7	
6:30	49	3	6		7:00	59	4	9	
6:45	51	5	4		7:15	60	1	8	
7:00	52	4	7		7:30	62	1	9	
7:15	52	4	3		7:45	62	3	9	
7:30	53	5	8		2:00 p.m.	75	0	3	
12:00	65	2	3		2:15	75	2	5	
12:15 p.m.	65	2	2		2:30	76	2	4	
12:30	66	0	3		2:45	77	1	2	
12:45	66	1	5		3:00	77	1	4	
1:00	65	3	4		3:15	78	3	5	
1:15	65	2	3		3:30	73	3	3	
1:30	66	0	4		6:45	73	2	2	
1:45	67	3	2		7:00	72	1	4	
2:00	68	1	3		7:15	70	2	1	
2:15	69	2	2		7:30	70	0	1	
2:30	70	2	4						

sagebrush community and very few were seen. During 1940 they were practically absent, only 2 being seen and one caught in White Valley from April to September. This decrease in their numbers from one year to the next was not a local occurrence restricted to White Valley, but was apparent throughout the surrounding areas. The cause for such a drop in abundance was not determined but it would appear as if a disease of some sort may have been responsible. Long (1940) states that in the southern part of the state large numbers of them were infected with a disease which caused open sores on their appendages and body.

Their burrows were most numerous along the banks of ravines although they also occurred in flat areas at the bases of the desert shrubs. Most of the young were almost full grown by the last of June although one half-grown young was caught July 26, 1939.

Unlike most desert rodents, this species is diurnal and remains active throughout the day. Its activity is not restricted to the ground and it was often seen in the top of the shrubs feeding on the leaf buds and ends of the stems. The highest shrubs of the area were also utilized as look-out posts. Their food consists mainly of green herbaceous material and shrubs, although insect fragments were found in 2 stomachs. They also fed on the carcasses of rodents of various kinds which the writer had skinned and discarded.

They remained active throughout the summer and gave no evidence of going into hibernation by the first part of September. Information from Civilian Conservation Corps workers indicates that they hibernate in late autumn and reappear very early in the spring. In the southern part of Utah and in New

Mexico, where the winters are mild, they seldom if ever hibernate (Long 1940, Bailey 1931).

Because of their diurnal habits this species forms an important part of the food supply of certain hawks such as the Swainson hawk and the prairie falcon. Their shallow burrows make them very easy prey of the badger and the kit fox and they also form part of the diet of the gopher snake and the rattlesnake.

Chipmunks, *Eutamias minimus consobrinus* (Allen), were encountered only in the sagebrush community in Fernow Valley. They were never numerous and occurred with a frequency of only 25 percent in the sample plots (Table 13).

The pocket gopher, *Thomomys bottae centralis* Hall, occurred throughout the various communities of White Valley. In most communities it was very scarce but in certain localities such as in the vicinity of Tule Springs and near the base of the Black Knolls they were rather common. None were found in the greasewood community except around the springs. Near these springs they were active throughout the summer but in the shadscale and other communities at higher elevations, they threw up mounds only during the early spring when the soil was moist.

This species is largely nocturnal, as far as foraging above ground is concerned, but it remains active throughout the day within its burrows. No animals were caught above ground except at night but they could be caught at any time of the day by placing traps in their burrows. The rate at which mounds were thrown up would indicate that they are most active underground during the early morning hours.

Because of their digging activities they play an important part in soil alteration. Grinnell (1923) estimated that 7.2 tons of earth per square mile are brought to the surface by them in Yosemite National Park, California each year and Ellison (1946) found

that approximately 5 tons of soil per acre is brought to the surface in the Wasatch Plateau of central Utah, by pocket gophers. They also alter the sub-surface composition of the soil and may be responsible for the penetration of hard-pans, thus bringing about changes in the composition of the vegetation such as are described on page 282. Their direct effects on the vegetation, through their foraging activities, was often very marked in the immediate vicinity of their burrow openings where the grass was clipped off even with the surface of the ground. Their subterranean feeding activities often kill many plants. At the Desert Range Experiment Station numerous bunches of rice grass were killed by their roots being eaten off just below the surface of the ground.

Young gophers about one-third grown were caught May 11 at Tule Springs and May 24 and 25 in the tetradymania community.

The relative abundance of ground squirrels and pocket gophers in the different communities was not determined because the traps used in making population studies of the other rodents were not suitable for catching these species. Whenever the writer refers to "total" rodent populations he is referring to populations exclusive of ground squirrels and pocket gophers.

Three species of pocket mice occurred in the communities studied. The most widely distributed species was the little pocket mouse, *Perognathus longimembris nevadensis* Merriam, which was taken in all communities except the black sage and sagebrush (Table 13). This species was only occasionally caught and was most abundant in the tetradymania community in areas where the soil texture varied from sand to medium gravel. A total of only 21 specimens were trapped of which 13 were males. Two pregnant females were taken May 22, one of which was carrying 6 embryos and the other 4.

TABLE 13. Distribution and relative abundance of rodents, exclusive of ground squirrels and pocket gophers, in the various biotic communities.

Species	Shadscale		Winterfat		*Ecotone		Greasewood		Tetradymania		Black Sage		Sagebrush	
	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total	No. per Hectare	Percent of Total
<i>Eutamias minimus</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3.0	5.5
<i>Perognathus parvus</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.3	0.6
<i>Perognathus formosus</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	0.5	1.2	8.8	21.3	.....	.....
<i>Perognathus longimembris</i> .....	1.3	3.1	0.5	1.6	.....	.....	.....	.....	1.3	3.1	.....	.....	.....	.....
<i>Dipodomys microps</i> .....	34.0	80.6	14.3	45.5	13.8	42.3	10.2	22.3	25.5	60.9	10.5	25.4	8.5	22.2
<i>Dipodomys ordii</i> .....	2.8	6.6	8.5	27.1	10.0	30.7	13.5	29.5	9.0	21.5	.....	.....	11.3	25.5
<i>Microdipodops megacephalus</i> .....	1.0	2.4	3.8	12.1	.....	.....	0.2	0.4	0.8	1.9	.....	.....	.....	.....
<i>Onychomys leucogaster</i> .....	0.3	0.7	0.5	1.6	.....	.....	0.7	1.5	0.3	0.7	.....	.....	.....	.....
<i>Reithrodontomys megalotis</i> .....	.....	.....	.....	.....	1.3	4.0	9.5	20.7	.....	.....	.....	.....	4.3	8.1
<i>Peromyscus maniculatus</i> .....	2.8	6.6	3.8	12.1	7.5	23.0	11.7	25.6	4.0	9.5	3.2	7.7	20.3	38.1
<i>Peromyscus crinitus</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	12.6	30.4	.....	.....
<i>Neotoma lepida</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	0.5	1.2	6.3	15.2	.....	.....
Totals.....	42.2	.....	31.4	.....	32.6	.....	45.8	.....	41.9	.....	41.4	.....	47.7	.....

\*Shadscale-Greasewood Ecotone Community.

In the black sage community the little pocket mouse was replaced by an ecological equivalent, the long-tailed pocket mouse, *Perognathus f. formosus* Merriam, which constituted 21.3 percent of the total rodent population (Table 13). This species also occurred in the tetradymia community in rocky situations at the base of the House Range. No pregnant females were caught but 4 immature specimens about two-thirds grown were taken in July, 1940.

The Great Basin pocket mouse, *Perognathus parvus olivaceus* Merriam, was taken only in the sagebrush community. This species occurred with a frequency of only 25 percent and constituted less than 1 percent of the total rodent population (Table 13).

One of the most prevalent minor influents of this biome is the kangaroo rat. Eleven geographic races of *Dipodomys microps* and at least 5 geographic races of *Dipodomys ordii* occur throughout Utah and Nevada (Hall & Dale 1939). Two species, *Dipodomys microps bonnevilliei* Goldman and *Dipodomys ordii celeripes* Durrant and Hall, were widespread throughout most communities studied, but the relative abundance and the frequency of occurrence of each varied from one community to another. *Dipodomys microps* occurred in all communities varying in frequency from 100 percent to 69.2 percent, whereas *Dipodomys ordii* occurred in all communities except black sage, but the frequency of occurrence of this species was considerably less than *microps* except in the winterfat, greasewood and sagebrush communities (Table 14).

TABLE 14. Frequency of occurrence (percent) and relative maximum, minimum, and average abundance of kangaroo rats per hectare in various biotic communities. (Results from 64 trapping plots.)

Biotic Communities	<i>Dipodomys microps</i>				<i>Dipodomys ordii</i>			
	Freq. Per cent	Abundance			Freq. per cent	Abundance		
		Max.	Min.	Ave.		Max.	Min.	Ave.
Shadscale.....	100	45	10	34.0	29.2	35	0	2.8
Winterfat.....	100	36	5	14.3	100	15	5	8.5
Tetradymia.....	100	40	5	25.5	33.3	20	0	9.0
Shadscale-Greasewood.....	100	25	10	13.8	80	15	0	10.0
Ecotone								
Greasewood.....	69.2	35	0	10.2	64.6	50	0	13.5
Black Sage.....	100	23	5	10.5	0	0	0	0
Sagebrush.....	75	28	0	8.5	87.5	33	0	11.3

*Dipodomys microps* was most abundant in the shadscale, tetradymia, winterfat, shadscale-greasewood ecotone, and black sage communities, whereas *Dipodomys ordii* was most abundant in the greasewood and sagebrush communities (Table 14). The distribution of these species seems to be very closely related to the texture of the soil. *Dipodomys microps* was most abundant where the soil consisted chiefly of medium to fine gravel, whereas *Dipodomys ordii* was most abundant in areas of fine gravel and sand or fine, loose clay loam soils (Table 15). The

digging ability of kangaroo rats as a whole is limited by their small fore feet and consequently loose soil which is fine in texture seems to be preferred by most species (Bailey 1931, Grinnell 1932, Hawbecker 1940, Hardy 1945). However, *Dipodomys microps* occurred all the way to the top of the Black Knolls where the soil was very rocky and shallow. Fine sand and loose clay soils not only seem to be preferred for burrows by many species but they are utilized to a great extent by kangaroo rats for taking "dust baths." When these rodents are kept in cages without such soil their fur becomes matted and oily in appearance within a very few days.

TABLE 15. Distribution of kangaroo rats in relation to soil texture. (Results from 64 trapping plots.)

Soil Texture	<i>Dipodomys microps</i>		<i>Dipodomys ordii</i>	
	Number per hectare	Frequency percent	Number per hectare	Frequency percent
Coarse gravel and large rocks.....	23.8	100.0	0	0
Medium to fine gravel.....	28.5	100.0	6.7	22.2
Fine gravel to sand.....	18.2	100.0	26.3	92.9
Sand (Occasional dunes).....	12.0	100.0	20.8	100.0
Clay (Surface baked).....	18.2	90.0	7.3	70.0
Clay (Loose and spongy).....	12.5	40.0	21.3	100.0

The abundance and kinds of vegetation are also important factors affecting the distribution of these rodents. In areas where the soil was very loose, the kangaroo rat mounds were almost invariably located at the bases of the larger shrubs. The roots of these plants presumably support the loose soils and help to prevent the kangaroo rat burrows from collapsing. Where the soils were more firm the burrows were not restricted to the bases of the plants. The greatest populations of kangaroo rats occurred in the shadscale community where the vegetation density was only about half of what it was in the greasewood and sagebrush communities. A maximum population of 103 kangaroo rats per hectare occurred in a sampling area within the shadscale community where the vegetation coverage was only 12.8 percent and where the soil texture varied from fine to medium gravel, whereas the maximum number taken per hectare in the greasewood community was 50, from a sampling area where the vegetation coverage was 21.4 percent and the soil was fine loose clay. The kinds of plants on which the kangaroo rats feed may also be an important factor in their distribution. Seventy-one percent of the rats that were harvesting food materials were found to be carrying shadscale leaves in their cheek pouches. As many as 210 leaves were found in the cheek pouches of one rat. Other food materials found in their cheek pouches included globemallow leaves (1%); winterfat leaves (3%); ephedra seeds (3%); Russian thistle seedling leaves (7%); and grass seeds (15%). Six scarabaeid beetles, *Diplotaxis* sp., were found in the cheek pouches of one rat together with shadscale leaves.



Since the examination of 72 stomach contents revealed nothing but vegetable materials, it is unlikely that these beetles are utilized as food, and it is presumed that they were accidentally placed in the pouches while the rat was harvesting shadscale leaves. Captive kangaroo rats readily stripped the leaves from shadscale stems and preferred them to any other vegetation. Whether this plant is utilized to a greater extent under natural conditions because it is actually preferred or whether it is so utilized because it is the plant most available was not satisfactorily determined, but the fact still remains that the greatest populations of kangaroo rats were attained within the shadscale community and shadscale leaves were found more often in their cheek pouches than the total of all other kinds of vegetation.

Much of the nocturnal activity of kangaroo rats is spent in harvesting and storing food materials. They constantly scurry about in search of food materials which they carry back to their mounds. Plant leaves were often placed in surface caches scattered about on their mounds outside the burrows. Small pits, 1 and 2 inches in diameter and about 1.5 inches deep, were excavated on the surface of the mounds and filled with harvested food materials. Some of these caches were lightly covered with soil while others were fully exposed. Bailey (1931) and Shaw (1934) have suggested that the purpose of these caches is to "cure" the food which is later removed to the burrows. Large piles of food materials were also occasionally encountered on the surface of the mounds. Within the greasewood community such piles consisted chiefly of *Atriplex nuttallii* leaves, the volume of one such food cache amounting to slightly less than 2 quarts. Another such cache in the tetradymia community consisted of ephedra seeds and had a volume of 1.5 quarts. Stored food materials found within their burrows consisted of various grass seeds, leaves of annual herbs, shadscale leaves, and ephedra seeds.

The breeding season of both species evidently begins in early spring. No pregnant females were trapped after the end of April. The differential occurrence of lactating and pregnant females and the occurrence of immature rats suggests that the breeding season of *Dipodomys microps* is slightly earlier than that of *Dipodomys ordii*. The last lactating females of the first species were taken April 16 whereas lactating females of the second species were taken as late as May 15. The maximum percentages of immature rats of both species occurred in May but the percentages were higher for *Dipodomys microps*. Although the percent of immature *Dipodomys ordii* were not as high during June as they were in May, they were higher than they were for *Dipodomys microps* (Table 16). The number of young per litter seems to vary from 2 to 4. Seven out of 11 pregnant females examined were carrying only 2 embryos and the other 4 were each carrying 4 embryos.

The sex ratio of trapped individuals was approximately even, being 49.8% males in *Dipodomys*

TABLE 16. Percentages of immature kangaroo rats trapped from May to August, 1940.

Months	<i>Dipodomys microps</i> <i>bonnerillei</i>			<i>Dipodomys ordii</i> <i>celeripes</i>			Combined Total
	Males	Females	Total	Males	Females	Total	
May.....	73.3	76.7	75.0	63.6	64.3	64.0	69.5
June.....	45.2	33.9	39.6	55.6	50.0	52.8	46.2
July.....	63.0	28.2	45.6	8.3	25.0	16.7	31.2
August.....	21.1	33.3	27.2	18.2	20.0	19.1	23.2

*microps* and 56.6% males in *Dipodomys ordii*. Individual kangaroo rats exhibit a very decided intolerance for each other and when placed in the same cage or when caught in the same live trap they would often fight until one of them was killed. This intolerance was exhibited not only between individuals of the same sex but also between the opposite sexes. Such intolerance is also evident from the fact that in many other species only one individual is found in each mound (Vorhies & Taylor 1922, Bailey 1931, Grinnell 1932, Monson & Kessler 1940). The number of mounds found in this study varied from 3 to 40 per hectare with an average of 16.8. This is slightly more than one mound per rat when compared with the trapping data, the average number of rats caught per hectare being 13.2. This difference may be due to the fact that not all of the rats were caught during four nights' trapping or to the possibility that some of the counted mounds were not occupied. It does indicate however, that the number of mounds may be used as a relative approximation of kangaroo rat populations.

Although the home range of the kangaroo rat was not determined there is evidence that the area over which it travels is rather large. One rat was caught on a barren playa 1046 feet away from the nearest vegetation and 1231 feet from the nearest burrow. Live trapping also indicated that there is a considerable shifting of individual rats in the same area from one time of the year to another. One 0.2-hectare plot was trapped with live traps for



FIG. 16. Kangaroo rat-winterfat interaction. Note increased height of winterfat plants on kangaroo rat mound, in center of photograph. (Aug. 14, 1940.)

5 consecutive nights from May 13 to 17 during which time 12 rats were caught, marked and released. This same plot was then retrapped with killer traps from August 29 to September 1. Although 16 rats were caught only 2 of them had been previously marked. The mortality and replacement of the marked rats must have been very high during the interval of time between the two trapping periods or most of the ones that were marked had come into the plot from adjacent areas and had failed to return at the time the area was retrapped.

The interactions between the kangaroo rats and other biotic components of the community are many and varied. Their herbivorous feeding habits result in the consumption of considerable quantities of plant materials in the form of leaves and seeds. The storage of these seeds may in turn aid in the distribution of the plants. It is quite possible that seeds in the surface caches may sprout and grow. Although the writer was unable to find any direct evidence for this coaction, Hawbecker (1940) has found grain seeds of such surface caches sprouting and growing. The role which burrowing rodents play in soil formation has been very widely recognized (Grinnell 1923, Formoson 1928, Taylor 1935). Kangaroo rats may not only influence the distribution of plants through their seed harvesting activities but they may also influence the growth of plants by altering the chemical and physical composition of the soil as a result of their burrowing activities. The actual excavation of burrows not only facilitates the penetration of water and oxygen to greater depths but it brings the subsoil to the surface where it is mixed with the topsoil and it tends to produce finer sized soil particles which increase the moisture equivalent values and waterholding capacity of the soils, thus actually increasing the amount of water available to the plants (Greene & Murphy 1932). Not only do these rodents alter the physical nature of the soil but through the production of excreta and the storage of plant materials in their burrows they also alter the chemical composition of the soil. Soils taken from the kangaroo rat mounds have been shown to contain greater quantities of soluble salts, especially calcium, magnesium, bicarbonate, and nitrate ions than soils adjacent to the mounds (Greene & Reynard 1932). These effects are often very noticeably reflected in the growth and development of the plants. This reaction was especially conspicuous in certain winterfat areas where the height of the plants in the vicinity of the kangaroo rat mounds was almost twice as great as in the adjacent areas (Fig. 16). Another effect of rodents on the distribution of winterfat was very noticeable in Antelope Valley. Within this valley there is a hard-pan so near the surface that winterfat is unable to establish itself because of the shallowness of the soil and the consequent lack of sufficient moisture. Such areas are occupied by the subdominant little rabbit-brush within which are interspersed small circular "islands" of winterfat (Fig. 14). Wherever these islands of winterfat occurred there were numerous

pocket gopher and kangaroo rat burrows. An investigation of the soil conditions in these places, by digging a transect through some of them, showed that within such islands the hard-pan had been broken and the roots of the winterfat were thus able to penetrate the soil to greater depths and thus obtain sufficient moisture to support the plant.

Kangaroo rat burrows are used by reptiles, especially lizards, as avenues of escape from their enemies, as a means of avoiding high summer temperatures, and as places in which to hibernate. The abandoned burrows are also utilized as places of abode by many invertebrates such as spiders, tarantulas, scorpions, and insects especially tenebrionid beetles.

Kangaroo rats also constitute a large part of the food supply of kit foxes, burrowing owls, badgers, and coyotes. Because of their nocturnal habits they are seldom taken by hawks but rattlesnakes and gopher snakes often prey on them by entering their burrows.

The kangaroo mouse, *Microdipodops megacephalus paululus* Hall & Durrant was consistently present only in the winterfat community where it occurred in 100 percent of the trapping plots. Its distribution seems to closely correlate with soil texture. Eighty percent of the total number caught were taken in areas of sandy soil. It was never abundant, even within the winterfat community, and comprised but a small part of the total rodent population (Table 13).

Little evidence of kangaroo mouse's food habits and time of reproduction was obtained. The cheek pouches of only two specimens contained food materials, one of which was carrying shadscale leaves and the other one Indian rice grass seeds. Two females, trapped May 4, each contained 4 embryos. The average number of embryos found in 37 females by Hall and Linsdale (1929) was 4 with a variation from 1 to 6. Thirty-five of these females were taken in May.

The ecological importance of this species is low because of its scarcity. This apparent scarcity may be due to the fact that the communities studied are on the eastern border of its range. Only 23 specimens were caught during the entire period of this investigation whereas 92 specimens were caught in 198 traps during one night in Lincoln County, Nevada, near the center of its range, by Hall and Durrant (1937). Such a population would greatly add to its ecological significance.

The grasshopper mouse, *Onychomys leucogaster brevicaudus* Merriam, occurred in most of the communities of White Valley (Table 13). Although only 10 specimens were caught this trapping data may not necessarily represent the true relative abundance of this species in comparison with the data for other rodents, because its food habits are so different. Since this species is largely insectivorous and carnivorous it is possible that the oatmeal bait, which was routinely used for baiting the traps, may not have been as attractive to it as to the herbivo-

rous species. Sand crickets comprised 66%; grasshoppers, 17%; beetles, 6%; lizards, 2%; and bait only 9% of the stomach contents from 6 specimens. The stomach containing the lizard (*Uta*) also contained 22 small ants which were thought to have probably been in the stomach of the lizard at the time it was eaten. The examination of 96 stomachs from 13 states by Bailey and Sperry (1929) shows that 79.28 percent of the food of this mouse consists of insects, chiefly orthoptera and coleoptera, and that vegetable materials comprise only 11.13 percent. They also found lizards (*Sceloporus* and *Uta*) in 3 stomachs.

The interactions between the grasshopper mouse and invertebrates and small rodents is probably greater than for any other small mammal of these communities. This mouse not only preys on invertebrates and small lizards but it also kills other rodents as large or larger than itself. Kangaroo rats and mice of other species caught in the same live trap with a grasshopper mouse were killed and partly eaten on several occasions.

The harvest mouse, *Reithrodontomys m. megalotis* (Baird), was found only in the greasewood, shadscale-greasewood ecotone, and sagebrush communities (Table 13). Within the greasewood community it was taken in 61.1 percent of the trapping plots and comprised almost 20 percent of the total rodent population. It was most abundant where the vegetation was most dense and was most frequently caught at the base of large shrubs.

The breeding season of this species is very extended. Pregnant and lactating females were taken in early September as well as in April and May. Immature specimens were also taken in early May.

The white-footed mouse, *Peromyscus maniculatus sonoriensis* (LeConte), is a very widespread species and occurred in all communities (Table 13). It was most abundant in the sagebrush and greasewood communities. The dominant shrubs of these two communities are very similar in vegetative form and provide more cover and nesting places for this species than do the dominant shrubs of the other communities.

The breeding season within the areas studied apparently occurs during early spring. No pregnant females were taken after the last of April and no lactating females were caught after the middle of May. The number of embryos varied from 3 to 6 with 4 being the most frequent number. Males were caught much more frequently than females, the number taken being 79 and 42 respectively. This may indicate that the home range of the males is much larger than it is in the females and they consequently come in contact with the traps more often than do the females.

In the black sage community *Peromyscus maniculatus* was largely replaced by another species of white-footed mouse, *Peromyscus crinitus pergracilis* Goldman (Table 13). This species was most abundant in very rocky areas especially in the vicinity

of ledges. No pregnant females were trapped but 6 immatures were caught during June and 1 in July.

The desert pack rat, *Neotoma l. lepida* Thomas, was largely restricted to areas where there are numerous large boulders and cliffs beneath which it builds its den. Its dens were very conspicuous because of piles of sticks and debris that are accumulated by the rats. One abandoned den was found in the greasewood community but no rats were caught except in the tetradymia and black sage communities. Within the tetradymia community these rats occurred only at the base of the House Range where there was an abundance of large rocks beneath which the dens were located.

This species was most abundant in the black sage community where it was caught in 75 percent of the trapping plots. The relative abundance of the pack rat (Table 13) is probably low because the Museum Special traps used were too small to hold all the rats that came in contact with them. Twenty-five percent of the traps set in the black sage community were frequently sprung, presumably by pack rats.

The pack rat apparently breeds throughout the spring, summer, and autumn. Pregnant or lactating females were taken during every month from April to September. A female captured in May with 3 suckling young gave birth to another litter of 4 in June while being kept in captivity. Five out of 8 pregnant females were carrying 3 embryos, one 4, and the remainder 2 each.

The black-tailed desert jack rabbit, *Lepus californicus deserticola* Mearns, is an important minor influent of all the biotic communities, but it was most abundant in the greasewood and sagebrush areas. (Tables 17 and 18.) The relative abundance of rabbits in the greasewood community by actual counts on 4-hectare plots was 6.7 times greater than in the shadscale community but the number of pellets found per square meter of ground surface was only 3.7 times greater. This difference seems to be a reflection of the daily activities of the jack rabbit. Counts made during mid-day tended to be higher in the greasewood community and lower in the more open types of communities such as shadscale and winterfat because the rabbits moved into the more dense vegetation within which they "shaded up" during the heat of the day. During the early morning hours and again in the evening the rabbits leave their resting "forms" and many of them move out

TABLE 17. Abundance of jack rabbits per 10-hectares based on counts made on 4-hectare plots.

Communities	Freq. (Percent)	Abundance		
		Max.	Min.	Average
Shadscale.....	17	1	0	0.75
Tetradymia.....	40	3	0	1.0
Greasewood.....	100	22	3	5.0
Sagebrush.....	100	19	2	4.3

into the more open communities to feed. Since most of the pellets are deposited while the rabbits are feeding their apparent relative abundance within the feeding areas tended to be greater when the pellet count method was used.

The number of pellets per sample in the shadscale community in White Valley average 2.2 while the number in the same type of community at the Desert Range Experiment Station was only 0.8 (Table 18). This difference is presumably due to a difference in the location of the two areas with respect to greasewood communities. The shadscale community in White Valley is adjacent to a greasewood area, whereas the shadscale community at the Desert Range Experiment Station is many miles from any greasewood area and consequently was not used as the forage ground by rabbits from any other community, as was the shadscale community of White Valley.

TABLE 18. Jack rabbit pellets per square meter of ground surface. 1, Samples taken at the Desert Range Experiment Station; 2, Samples taken in vicinity of Tule Springs; 3, Samples taken around border of Tule Springs.

Communities	Samples taken	Freq. (Percent)	Abundance		
			Max.	Min.	Ave.
Shadscale <sup>1</sup> .....	220	27.6	22	0	0.8
Ungrazed area..	104	40.4	22	0	1.4
Open Range.....	116	15.5	6	0	0.3
Shadscale.....	240	35.0	19	0	2.2
Winterfat <sup>1</sup> .....	226	11.4	9	0	0.3
Ungrazed area..	192	19.8	9	0	0.6
Open Range.....	134	6.0	6	0	0.1
Tetradymia.....	174	38.0	8	0	1.4
Greasewood.....	240	95.0	51	0	8.2
Greasewood <sup>2</sup> .....	200	100.0	47	1	10.5
Salt grass <sup>3</sup> .....	20	100.0	414	66	280.0
Sagebrush.....	128	97.0	39	0	8.0

Pellet counts were considerably higher in the shadscale and winterfat communities at the Desert Range Experiment Station which had not been grazed than they were in the same types of communities which had been subjected to grazing (Table 18). Observations on the feeding activities of jack rabbits by the writer indicate that they prefer grass when it is available. Since grasses were more abundant within the protected areas it would appear as if that was one of the factors responsible for the higher pellet counts. The salt grass areas near Tule Springs were favorite feeding grounds of many rabbits from adjacent areas. Distinct, heavily trodden trails led into these grassy areas from all directions. Rabbits would begin to come to these grassy areas near sundown and as many as 11 were observed feeding at the same time in an area less than one-half acre in size.

Young jack rabbits about one-fourth grown were seen as early as May 1 and young ones just a few days old were observed during the latter part of

June. Although more than one litter may be produced during the spring and early summer there was no evidence that young were born after the first of July. Young jack rabbits were never found in a nest but always occurred alone, concealed beneath a shrub. They escape notice by remaining perfectly motionless and will not move unless one practically comes in contact with them. The number per litter varies from 1 to 6 with an average of about 2.5 (Vorhies & Taylor 1933). Only 2 pregnant females were examined, one of which contained 5 embryos and the other 6.

The jack rabbit is a very important influent because of its effects on the vegetation which it utilizes as food and because it is an important source of food for many of the predatory mammals and birds. Vorhies & Taylor (1933) estimate that 30 rabbits consume as much forage as one sheep or 148 eat as much as a cow. A large number of plants are utilized as food, grasses of all kinds seeming to be highly preferred. Many of the grasses which have been greatly reduced in abundance by over-grazing are now eaten by the rabbits before the sheep arrive in the autumn. Within some areas practically every globemallow was clipped off about 6 to 8 inches above the ground just at the time they were beginning to blossom. If this plant were not a perennial, such consumption would soon greatly decrease its abundance. Shadscale, winterfat, and greasewood were all used as food. The greasewood seemed to be eaten more often than the other two, probably because the rabbit population was higher where it was present. The lower branches were usually cut off about 4 or 5 inches back from their tips and all but about an inch of the tip eaten. *Atriplex nuttallii* seemed to be one of their favorite foods especially during late summer. The remains of this plant in the spring also gave evidence that it had been greatly utilized during the winter. In many instances the stems were cut off at the root crown below the surface of the soil. In such cases the ends of the stems were not eaten and stems 5 to 6 inches long were strewn about the surface of the ground. Pickleweed was occasionally eaten during mid-summer. This plant was usually cut off about 2 inches below the surface of the ground and only the most succulent lower 2 or 3 inches of the stems eaten.

Cottontails, *Sylvilagus nuttallii grangeri* (Allen), were found regularly only in the tetradymia, black sage, and sagebrush communities. Within these communities there were either large rocks, crevices, or ravines which afforded them protection. They were never numerous and averaged only 2.8 individuals per 10 hectares in the tetradymia community and 0.5 in the sagebrush. Although their pellets were found in shadscale areas adjacent to the tetradymia, they were never encountered in the shadscale census areas.

The young reared in an old badger excavation, were seen for the first time May 18. Several young one-third to one-half grown were observed in the



early part of June. Because of their scarcity their ecological importance is not very great within the communities studied.

### Birds

Most of the minor influent birds are wide-ranging and occurred in more than one community. The birds occurring in the shadscale tetradymia, and winterfat communities are very similar, presumably because the dominant plants of these communities are low, sparse, and similar in vegetative form. The writer has combined his general cruising data for these three communities and whenever a reference is made to the birds of the shadscale it is to be understood that such a reference also includes the tetradymia and winterfat communities unless otherwise stated.

A total of 61 species of birds were observed during the course of this investigation (Appendix A) of which 52 species have been arbitrarily designated as minor influents. Summer residents which occurred in all communities included the following:

Turkey Vulture, *Cathartes aura teter* Friedmann  
Mourning Dove, *Zenaidura macroura marginella* (Woodhouse)

Summer vagrant in all communities except sagebrush.  
Arkansas Kingbird, *Tyrannus verticalis* Say

A summer vagrant except in the vicinity of buildings.  
Horned Lark, *Otocoris alpestris utahensis* Behle  
Raven, *Corvus corax sinuatus* Wagler

Sage Thrasher, *Oreoscoptes montanus* (Townsend)

Summer vagrant in shadscale communities.

Shrike, *Lanius ludovicianus nevadensis* Miller

Cowbird, *Molothrus ater artemisiac* Grinnell

Never abundant in any community.

Desert Black-throated Sparrow, *Amphispiza bilineata deserticola* Ridgway

Most abundant in shadscale community.

Sage Sparrow, *Amphispiza belli nevadensis* (Ridgway)

Summer vagrant in shadscale community.

Brewer Sparrow, *Spizella breweri breweri* Cassin

Summer vagrant in shadscale community.

The turkey vulture was only occasionally seen, but it was observed throughout the summer in one community or another. The sharp-shinned hawk, *Accipiter striatus velox* (Wilson), was seen only twice and is considered a minor influent because of its scarcity.

Mourning doves nested only in the sagebrush area and were seen only infrequently in other communities, being most prevalent during late August and early September. Their breeding season was very prolonged and more than one brood of young was evidently produced each year. Nests containing eggs were found in May and as late as August 4 in the sagebrush community.

Nighthawks, *Chordeiles minor* ssp., were seen with a frequency of 34.8 percent in the sagebrush community but were seldom seen in other areas. The Nuttall poor-will, *Phalaenoptilus n. nuttallii* (Audubon), was occasionally flushed in the shadscale community in August but was encountered only once in the sagebrush community.

Although ravens and sparrow hawks nested in the adjacent mountains they foraged throughout all the valley communities and are thus considered summer residents. During their nesting period the ravens made several trips to the valleys each day in search of food. After the young were able to fly the family groups would come down into White Valley about 5:00 to 6:00 a.m. and remain throughout the day, returning to the mountains about sundown. They were especially prevalent along roads where they fed on rabbits, rodents, and reptiles that were killed by passing automobiles. Sparrow hawks occurred most regularly near cultivated areas and were most abundant during late summer.

The horned lark, rock wren, *Salpinctes o. obsoletus* (Say), and the desert black-throated sparrow were the only species observed nesting the shadscale and associated edaphic communities (Table 19).

TABLE 19. Number and percentages of nesting, summer resident and transient minor influent birds. 1, Includes species observed in Tetradymia and Winterfat Communities; 2, Includes species observed at Tule Springs; 3, Percent of total species observed in all communities.

Communities	Nesting species		Summer residents		Transients		Total species <sup>3</sup>	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Shadscale <sup>1</sup> .....	3	9.4	16	50	16	50	32	61.5
Greasewood <sup>2</sup> .....	7	21.7	18	56.2	14	43.8	32	61.5
Sagebrush.....	5	14.8	21	61.8	13	38.2	34	65.4

Horned larks were most prevalent in the more open shadscale community and nested in the greasewood and sagebrush areas only where the vegetation was low and sparse. Their nests were always placed on the ground in a shallow excavation beneath some low-growing shrub. The only nest found in the greasewood community was beneath a small suaeda bush in an open sparsely vegetated area.

The breeding activities of the desert black-throated sparrow were almost entirely restricted to the tetradymia community. Only one late nest, located July 13, was found within the greasewood area (Table 20). This species seems to prefer an open type of vegetation within which there are occasional larger shrubs. These larger shrubs were used as nest sites and as singing perches by the males. Nesting pairs were usually well isolated from each other. All nests found were more than 50 meters apart. Both males and females incubated the eggs and fed the young. After the brooding of the nestlings was no longer necessary, the male and female usually remained very close together when foraging for food, seldom getting more than a few feet apart. They would return to the nest with food at the same time and take their turn in feeding the young. After the young left the nest the family remained very close together and moved about as a group. Their feeding activities were restricted to the shrubs where they

TABLE 20. Nesting records of birds within communities of White Valley, 1940.

Dates	Community	Plant in which nest was located	Position of nest on plant	Number of eggs	Remarks	
					Eggs hatched	Young left nest
DESERT BLACK-THROATED SPARROW						
April 22.....	Tetradymia	Ephedra	Southeast	4	April 30	May 11
May 8.....	"	Tetradymia	Northeast	4	Unknown	About May 30
" 12.....	"	Ephedra	North	3	May 20-21	?
" 19.....	"	Tetradymia	Northeast	?	4 young 3 to 4 days old	May 26
" 19.....	"	Sagebrush	"	3	May 31 and June 1	Young dead in nest June 10
" 21.....	Shadscale	Shadscale	"	3	Unknown	June 9
June 8.....	Tetradymia	"	"	3	All eggs failed to hatch	
July 13.....	Greasewood	Greasewood	North	3	Only 2 eggs hatched	One young found dead July 20
HORNED LARK						
May 17.....	Shadscale	Beneath Shadscale	East	4	May 23	About June 5
" 28.....	"	Beneath Shadscale	"	4	Eggs unhatched June 2	
June 7.....	"	Beneath Winterfat	"	3	Eggs not hatched. Female caught in trap	
" 9.....	"	Beneath Shadscale	"	3	June 13	June 25
" 17.....	Greasewood	Beneath Suaeda	North	?	Nest empty when found	
SAGE SPARROW						
May 14.....	Greasewood	Greasewood	North	4	May 21	June 3
" 17.....	"	"	"	3	May 21-22	June 2
" 17.....	"	"	East	?	Nest contained 3 young when found	
" 19.....	"	"	North	?	Nest contained 2 young when found	
BREWER SPARROW						
May 14.....	Greasewood	Greasewood	North	4	May 19	Unknown
" 15.....	"	"	East	?	Nest contained 4 young when found	
" 19.....	"	"	North	?	Nest contained 3 young when found	
GREAT BASIN SHRIKE						
May 16.....	Greasewood	Greasewood	Center of bush	0	Nest newly constructed	
" 20.....	"	"	"	1		
" 24.....	"	"	"	5		
" 25.....	"	"	"	6		
June 9.....	"	"	"	3	3 eggs hatched	
" 10.....	"	"	"	1	5 eggs hatched	
" 14.....	"	"	"	0	6 young	Nest empty June 28

foraged for insects. The breeding season of this species was very extended and probably more than one brood is produced. Nests containing eggs were found as early as April 22 and as late as July 13. The late nests contained fewer eggs and were less successful than the earlier ones (Table 20).

Rock wrens were found nesting only in the tetradymia community near the base of the mountains. One pair nested in a badger excavation and two others beneath large boulders.

The mockingbird, *Mimus polyglottos leucopterus* (Vigors), was never seen in the shadscale community and was only rarely encountered in other areas. It was seen most frequently in the sagebrush community where it occurred with a frequency of only 8.6 percent.

Sage thrashers, shrikes, sage sparrows, and Brewer sparrows, were only occasionally encountered outside the greasewood and sagebrush areas. The vegetation of these two communities is very similar in height, density, and form, and seemed to be pre-

ferred by these species. Nests of all but the sage thrasher were found, however, the activities and distribution of the adults and the occurrence of young sage thrashers indicated that this species also nests in these communities. Nesting sage sparrows and Brewer sparrows avoided the most dense vegetation and built their nests 10 to 18 inches above the ground in medium-sized shrubs which were well spaced. The only shrike nest found was located in the center of a large greasewood 2.5 feet above the ground and was so surrounded by upright branches that the incubating bird had difficulty in making a quick exit when the nest was approached.

The feeding activities of these sparrows and the sage thrasher were restricted to the shrubs where they fed on insects. Shrikes not only fed on insects, principally grasshoppers, but preyed on lizards as well. Their characteristic habit of impaling their prey was very much in evidence at the Desert Range Experiment Station where lizards (*Uta*) grasshoppers and sand crickets were found hanging

TABLE 21. Minor influent bird populations of a 4-hectare (10-acre) plot within the Shadscale Community.

Species	April			May					June				July			August			Sept.
	13	23	28	1	6	14	24	29	8	13	19	27	1	12	21	9	18	27	2
Sparrow Hawk.....	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..	1	..
Horned Lark.....	4	3	5	3	..	4	3	3	3	2	..	5	4	3	..	3	2	5	3
Raven.....	..	..	2	..	1	..	1	..	..	2	..	..	..	..	3	1	..	..	2
Vesper Sparrow.....	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Black-throated Sparrow.....	1	2	1	4	2	..	..	1	..	..	3	..	..	..	..	..	..	..	..
Sage Sparrow.....	..	..	..	..	1	..	..	..	..	1	..	..	..	..	..	..	..	..	..
Chipping Sparrow.....	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Brewer Sparrow.....	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Total.....	9	8	8	7	4	4	4	4	4	5	3	5	4	3	3	4	3	5	6

from the barbs along barbed wire fences. Grasshoppers were also found impaled on the thorns of greasewoods. The shrikes also fed on mice which had been caught in the writer's traps.

Summer resident species within the greasewood community which were restricted to the immediate vicinity of Tule Springs included the killdeer, *Charadrius vociferus vociferus* Linnaeus, the western yellow-throat, *Geothlypis trichas occidentalis* Brewster, the yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Bonaparte), and the red-winged blackbird, *Agelaius phoeniceus* ssp. A pair of killdeers nested near the edge of the spring but their nest could not be located. Four young were first seen June 8 at which time they appeared to be several days old. The yellow-throats and blackbirds remained at the spring throughout the summer and their spring activities indicated that they might nest but no nests or young were ever observed. The vegetation growing in the spring was greatly disturbed by a small herd of cattle which frequented the area and which probably prevented these birds from nesting during the summer of 1940.

Bird populations were relatively low in all communities. The average summer population, as determined from actual counts on 4-hectare (10-acre) plots, varied from 10.6 per 10 hectares (25 acres) in the shadscale and 12.6 in the tetradymia to 27.0 in the greasewood community. Populations were greatest in the tetradymia and shadscale communities dur-

ing the spring and early summer. A pronounced decrease occurred in the tetradymia community after the last part of June when the black-throated sparrows moved out (Table 22). This decrease coincided with a very rapid decline in the insect population (Fig. 9). The bird population of the shadscale community remained fairly constant throughout the summer being highest during April when several migrating species were present (Table 21). There was a general increase in bird population of the greasewoods during late summer (Table 23). The vegetation of this community was much taller and more dense than the vegetation of the shadscale and tetradymia communities and thus provided a greater amount of protection for the birds during hot summer months. The insect population of this community was also maintained at a more constant level (Fig. 9), so that the amount of food available to the birds was greater than in the other communities of White Valley.

Brewer blackbirds, *Euphagus c. cyanocephalus* (Wagler), vesper sparrows, *Poocetes gramineus confinis* Baird, and the white-crowned sparrows, *Zonotrichia leucophrys* ssp., were the only transient species which occurred in all communities. Transient and vagrant species of the shadscale community comprised 59 percent of the total number of birds seen. Many of these such as the Arkansas kingbird, ash-throated flycatcher, *Myiarchus c. cinerascens* (Lawrence), Say phoebe, *Sayornis saya saya* Bonaparte, sage thrasher, shrike, yellow-headed blackbird, red-

TABLE 22. Minor influent bird populations of a 4-hectare (10-acre) plot within the Tetradymia Community.

Species	April		May								June					July			August				Sept.
	14	23	2	5	7	15	19	23	28	30 <sup>a</sup>	9	12	19	20	26	2	13	22	1	9	17	26	3
Horned Lark.....												1		3			2	1	2	1	1	1	
Raven.....														2			1	1					
Rock Wren.....	2	1	1	1		1		2	1		2		4							1		1	
Desert Black-throated Sparrow.....	7	3	9	5	4	2	1	3	6	3	2	3	5				1						
Sage Sparrow.....																			1	1		1	
Chipping Sparrow.....	2																						
Brewer Sparrow.....																				1	1		2
White-crowned Sparrow.....	1		1																				
Total.....	12	4	11	6	4	3	1	5	7	3	4	4	9	5	0	1	3	2	3	4	2	3	2

TABLE 23. Minor influent bird populations of a 4-hectare (10-acre) plot within the Greasewood Community.

Species	April			May				June				July					August				Sept.
	16	23	28	7	13	16	24	1	8	14	26	2	10	13	18	26	5	12	18	27	4
Horned Lark...	1	..	2	3	2	..	3	7	4	6	2	2	6	5	3	1	9	7	12	19	12
Sage Thrasher...	..	..	..	..	..	1	1	..	..	..	1	1	..	..	..	..	..	3	..	..	2
Shrike...	1	..	..	..	1	1	..	..	..	..	1	1	..	..	..	1	..	..	2	1	..
Vesper Sparrow...	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
Black-throated Sparrow...	..	..	..	..	..	..	..	..	..	..	1	..	1	2	2	2	..	2	1	..	..
Sage Sparrow...	5	2	4	2	2	2	..	1	5	1	..	4	4	6	2	7	5	2	3	..	5
Brewer Sparrow...	3	2	1	2	3	3	1	2	1	3	1	1	..	..	1	1	1	..	..	1	1
Total...	10	4	7	7	8	7	5	10	10	10	6	9	11	13	8	12	15	15	18	21	20

winged blackbird, cowbird, house finch, *Carpodacus mexicanus* ssp., pale goldfinch, *Spinus tristis pallidus* Mearns, lark sparrow, *Chondestes grammacus strigatus* Swainson, sage sparrow, chipping sparrow, *Spizella passerina arizonae* Coues, and Brewer sparrow are summer residents of other valley communities. Vagrants from adjacent mountain communities included the white-throated swift, *Aëronauts s. saxatilis* (Woodhouse), rufous hummingbird, *Selasphorus rufus* (Gmelin), and the violet-green swallow, *Tachycineta thalassina lepida* Mearns.

The springs within the greasewood community not only attracted such transient waterfowl and shorebirds as the Treganza great blue heron, *Ardea herodias treganzai* Court, common mallard, *Anas p. platyrhynchos* Linnaeus, sora rail, *Porzana carolina* (Linnaeus), and the western sandpiper, *Ereunetes mauri* Cabanis, but they were also frequented by a number of other species including the barn swallow, *Hirundo rustica erythrogaster* Boddaert, yellow warbler, *Dendroica aestiva* ssp., Audubon warbler, *Dendroica auduboni* ssp., long-tailed chat, *Icteria virens auricollis* Bonaparte, green-tailed towhee, *Oberholseria chlorura* (Audubon), savannah sparrow, *Passerculus sandwichensis nevadensis* Grinnell, and the song sparrow, *Melospiza melodia* ssp.

Transient and vagrant minor influent birds seen in the sagebrush community included the broad-tailed hummingbird, *Selasphorus p. platycercus* (Swainson), magpie, *Pica pica hudsonia* (Sabine), piñon jay, *Cyanocephalus cyanocephalus* (Wied), rock wren, mountain bluebird, *Sialia currucoides* (Bechstein), western gnatcatcher, *Poliophtila caerulea amoenissima* Grinnell, green-tailed towhee, lark sparrow, chipping sparrow and the slate-colored fox sparrow, *Passerella iliaca schistacea* Baird.

#### Reptiles

Reptiles are very important and conspicuous seasonal minor influents within all the biotic communities studied. The following 6 species of lizards and 4 species of snakes were observed during the course of the investigation:

Collared Lizard, *Crotaphytus collaris baileyi* (Stejneger)  
Leopard-lizard, *Crotaphytus wislizenii* Baird and Girard

Brown-shouldered Uta, *Uta s. stansburiana* (Baird and Girard)

Sagebrush Lizard, *Sceloporus g. graciosus* (Baird and Girard)

Desert Horned-toad, *Phrynosoma platyrhinos* Girard

Whip-tail Lizard, *Cnemidophorus t. tessellatus* (Say)

Striped Racer, *Coluber t. taeniatus* (Hallowell)

Gopher-snake, *Pituophis catenifer deserticola* Stejneger  
Long-nosed Snake, *Rhinocheilus lecontei* Baird and Girard

Rattlesnake, *Crotalus viridis lutosus* (Klauber)

An attempt was made to estimate the relative abundance of the lizards by making counts within 0.4-hectare (1-acre) plots which were also used in making rodent population studies. The results of these counts for 3 communities in White Valley during the summer of 1940 are graphically represented in Figure 17, in terms of numbers of lizards per 10 hectares (25 acres). Although the results obtained include only those counts which were made during the morning and late afternoon hours in which the lizards were observed to be most active, they probably are lower than the actual total populations because most species tend to remain concealed beneath the shrubs and consequently escape observation. However these results do indicate relative differences in the abundance of the various species from one community to another and seasonal variations in the activity of the same species. Inasmuch as the vegetation of the greasewood community was much more dense than in other communities it is possible that more of the lizards were overlooked and their relative abundance within that community should be greater than the results obtained from this censusing method indicate. The data obtained indicate that the greatest lizard populations occurred in the tetradymia community where they varied from 91 lizards per 10 hectares in May to 29 in August with a summer average of 65.

The collared lizard was found only where there were large rocks and was consequently confined to the tetradymia and black sage communities. It was less numerous than any other lizard and was never observed within the census plots. The males were always well isolated indicating that they probably maintain individual territories of considerable size.



These lizards remained active throughout the day and were frequently seen on the top of large rocks even during the heat of the day when the surfaces of the rocks were very hot. Prolonged observations revealed that they do not remain on the exposed surface of these hot rocks for periods of more than 8 to 12 minutes at a time without moving into the shade.

The scarcity of these lizards and the difficulty involved in collecting them made it impossible to check very closely on their time of reproduction. Three females collected May 20 each contained 4 eggs varying from 9 to 12 mm. in length. No other females were collected until mid-July at which time they contained no eggs. The only young lizard seen was collected August 25. A captive female of a different subspecies, *Crotaphytus collaris collaris* (Say), which has a more southerly distribution than *baileyi*, is reported by Greenberg (1945) to have deposited 8 eggs May 14 after having been observed in copulation several times from April 15-23.

TABLE 24. Stomach contents of 8 specimens of *Crotaphytus collaris baileyi* (Stejneger).

	Percent of total volume	Frequency (Percent)
Brown-shouldered uta.....	36.6	25.0
Scorpion.....	9.2	12.5
Aceridae.....	3.0	12.5
Other Orthoptera.....	20.3	12.5
Tenebrionidae.....	3.8	12.5
Scarabaeidae.....	16.9	12.5
Curculionidae.....	4.8	25.0
Other Coleoptera.....	2.1	25.0
Coleoptera larvae.....	1.2	12.5
Unidentified insect fragments.....	2.1	25.0
Vegetation fragments.....	Trace	12.5

The collared lizard was found to feed primarily on other lizards and large insects (Table 24). The remains of brown-shouldered utas constituted 36.6 percent of the total food volume and occurred in 25 percent of the stomachs examined. Orthoptera made up 23.3 percent and coleoptera 28.8 percent of the total food from 8 stomachs.

The leopard-lizard is one of the most ecologically important lizards encountered because it occurred throughout all communities and because it feeds on such a variety of biotic components within the communities. It was not seen until April 26 and did not occur in any of the census plots until early May. It was most frequently observed in areas of fine gravel or sand and was most abundant within the census plots during late May, June, and July (Fig. 17). It was seen only infrequently before 7 o'clock in the morning and was most active from 9:00 a.m. until about noon and again during late afternoon.

This lizard moves very rapidly when frightened and on two occasions was observed to use only its hind legs when traveling at top speed. The ability

and speed with which it moves about enables it to readily capture other lizards and the larger insects which form a large portion of its diet (Table 25). Lizards, primarily utas, constituted almost 25 percent of the total food volume and occurred in 30 percent of the stomachs examined. The stomach of one large female contained a whip-tail lizard 9 inches in length. Eight different species of lizards, including members of its own species and the horned-toad are listed by Van Denburgh (1922) as the prey of this lizard. The larger insects such as grasshoppers and beetles, especially tenebrionids, comprised 53.3 percent of the total food volume in 20 stomachs. Grasshoppers occurred in 48 percent of the stomachs and beetles in 52 percent. The hymenoptera and diptera consisted primarily of the larger forms such as wasps and asilids. Lizards kept in captivity would eat as many as 5 medium sized grasshoppers in rapid succession but would take them only if they were moving. They could be induced to take dead grasshoppers only if they were moved mechanically. A few fragments of vegetation and also a few pebbles were found in some of the stomachs examined but they were believed to have been accidentally ingested while the lizards were capturing insects. However, Merriam (1893) found that blossoms and plant leaves were eaten by this lizard during early spring.

TABLE 25. Stomach contents of 20 specimens of *Crotaphytus wislizenii* Baird and Girard.

	Percent of total volume	Frequency (Percent)
Lizards.....	22.6	30.0
Araneida.....	0.4	5.0
Aceridae.....	21.2	45.0
Other Orthoptera.....	1.3	5.0
Heteroptera.....	0.4	5.0
Cleridae.....	0.5	5.0
Tenebrionidae.....	25.8	30.0
Scarabaeidae.....	2.7	15.0
Curculionidae.....	1.6	5.0
Coleoptera larvae.....	0.2	5.0
Lepidoptera larvae.....	1.3	15.0
Formicidae.....	0.3	5.0
Other Hymenoptera.....	8.1	25.0
Asilidae.....	8.2	10.0
Other Diptera.....	2.3	15.0
Unidentified insect fragments.....	3.1	20.0
Vegetation fragments.....	Trace	10.0
Pebbles.....	...	30.0

Sexual dimorphism is very marked in the leopard-lizard, especially when the females are gravid. The males are usually smaller than the females and the ventral surface and the sides of the tail of the gravid females often become a deep salmon red in color with red spots occurring along the sides of the abdomen. Copulating pairs were observed in White Valley during the last week in May. Merriam (1893) found them copulating May 17 to 19 in the vicinity of the Escalante Desert. All females examined before May 20 contained eggs but no

gravid females were found after the last of June (Table 26). The number of eggs per female varied from 4 to 5. The first newly hatched young were seen August 12, 1939 and August 11, 1940, after which dates they occurred rather frequently often being seen in greater abundance than the adults, especially within the shadscale community.

The brown-shouldered uta was consistently the most prevalent lizard in all communities. They were most numerous in gravelly areas where there was an abundance of large rocks and were consequently most abundant within the tetradymia community at the base of the House Range where they comprised 92 percent of the total lizard population in April and 63.6 percent of the average summer population. They became progressively less abundant from the base of the mountains to the valley floor.

The seasonal activity of the utas was longer than that of any other lizard encountered. They evidently came out of hibernation at an earlier date than most other species because they were most abundant during late April and early May whereas other species became most abundant during the latter part of May. They were also consistently more prevalent than other species during late summer. They likewise became active earlier in the day than most other species. During midsummer they were found to be active as early as 5:00 a.m., at which time other lizards were rarely seen. The reason for this interesting phenomenon is discussed later.

TABLE 26. Percentages of four species of gravid female lizards from April 15 to July 1, 1940.

Time of Year	SPECIES			
	Uta	Horned-toad	Leopard-Lizard	Whip-tail Lizard
April 15.....	100.0	—	—	—
20.....	78.0	—	—	—
May 1.....	80.0	100.0	—	—
10.....	66.7	100.0	100.0	100.0
20.....	63.0	75.0	100.0	100.0
June 1.....	25.0	86.0	75.0	72.5
10.....	0	37.5	33.3	90.0
20.....	0	0	0	25.0

No gravid females were found after the first of June indicating that the breeding season of this species is earlier than that of other lizards (Table 26). Gravid females have been found as late as June 20 in areas farther north within the Great Basin (Taylor 1912). The number of eggs per female varied from 3 to 5 with an average of 4.1, which is less than for any other species of lizard examined. Young utas were first seen July 7, 1939 and July 1, 1940. Two individuals collected July 1, were each 53 mm. in length and had so recently emerged from the eggs that the yolk sacs were still visible through the skin of their abdomens. During late July and throughout August the young utas were very prevalent and were often seen in greater abundance than the adults.

TABLE 27. Stomach contents of 17 specimens of *Uta stansburiana stansburiana* (Baird & Girard).

	Percent of total volume	Frequency (Percent)
Acarina.....	0.6	11.7
Araneida.....	6.6	35.3
Acrididae.....	24.3	23.5
Homoptera.....	1.8	11.7
Hemiptera.....	6.7	52.9
Cleridae.....	1.8	17.6
Tenebrionidae.....	1.8	5.9
Scarabaeidae.....	3.6	11.7
Other Coleoptera.....	1.8	17.6
Coleoptera larva.....	6.6	23.5
Lepidoptera larvae.....	3.7	11.7
Formicidae.....	22.3	76.5
Other Hymenoptera.....	1.9	5.9
Diptera.....	2.4	11.7
Unidentified insect fragments.....	14.1	47.0

The brown-shouldered uta feeds on both terrestrial and shrub-inhabiting insects. Ants, principally, *Formica* sp. and *Camponotus* sp., occurred more frequently in the stomachs examined than any other kind of insects and constituted 22.3 percent of the total stomach contents (Table 27). Grasshopper nymphs made up a slightly higher percent of the total food volume than ants because of their size, but they occurred less frequently. Coleoptera larvae and adults occurred with about the same frequency as ants but their total volume was less. The hemiptera consisted primarily of plant bugs and pentatomids. The homoptera were chiefly cicadellids, but chermids and coccids also occurred in some stomachs. These soft-bodied heteroptera are probably digested at a faster rate than other insects with more chitinous exoskeletons, such as grasshoppers and beetles, and the chances of finding their remains in the lizard stomachs would be much less even though they may constitute a much greater percentage of the food eaten than the stomach analysis would indicate. Knowlton (1932) found as many as 83 beet leafhoppers in one uta stomach with an average of 12.79 for 86 stomachs. The occurrence of lepidoptera was low and only larvae were found. Other arthropods eaten included spiders and mites but they constituted a small part of the total food volume. Other investigations (Knowlton & Janes 1931, and Woodbury 1932) also indicate that the consumption of spiders is low.

Utas were observed feeding on grasshoppers and ants in the field, and when kept in captivity they readily ate small grasshoppers, leafhoppers, flies, and ants. This lizard is not only important in the biotic relationships of the community because of the variety of invertebrates upon which it feeds, but it is in turn preyed upon by other reptiles, by birds, and to a limited extent by mammals.

Sagebrush lizards occurred only in the greasewood and sagebrush communities. They usually remained within the larger shrubs and were seldom seen in the open. They were very hesitant about going from one

shrub to another and would often remain within the same shrub until it was almost torn apart. The apparent relative abundance of this species was always low (Fig. 17). Inasmuch as this lizard was so restricted to the shrubs there would be a much greater chance for error in estimating its abundance than there would be in the case of other species which frequented open areas and which were found in communities where the cover was much less dense. Consequently the sagebrush lizards were probably much more abundant than the census method used would indicate. No quantitative data were obtained for the sagebrush community but general cruising observations indicated that this lizard was probably more abundant there, especially along the sides of ravines, than it was in the greasewood community.

TABLE 28. Stomach contents of 13 specimens of *Sceloporus graciosus graciosus* (Baird & Girard).

	Percent of total volume	Frequency (Percent)
Aceridae.....	24.8	46.1
Other Orthoptera.....	4.5	7.7
Homoptera.....	49.6	30.8
Hemiptera.....	1.6	7.7
Tenebrionidae.....	1.2	15.4
Scarabaeidae.....	4.1	23.1
Formicidae.....	4.1	100.0
Other Hymenoptera.....	4.0	15.4
Unidentified insect fragments....	6.1	76.5

Unlike many of the other lizards, which spent most of their time on the ground or among rocks, this species spends most of its time within the vegetation and was often seen in the very tops of large shrubs. The fact that these lizards frequent the shrubs is very prominently reflected by the kinds of insects found in their stomachs. Insects from shrubs such as homoptera, hemiptera, and orthoptera composed the greater part of their stomach contents (Table 28). Although ground beetles were very numerous within the greasewood community, they formed less than 2 percent of the total food volume. Ants occurred in all stomachs examined but comprised only 4.1 percent of the total food volume.

Although the reproductive organs of only a few females were examined the results obtained indicate that the eggs of the sagebrush lizard are probably laid during May or early June. Two females collected May 15 both contained well-developed eggs. One of them was carrying 8 eggs, 8 mm. by 13 mm. in size and the other 7 eggs, 9 mm. by 13 mm. in size. Three females collected June 30 contained only ova about the size of a pin head and were assumed to have deposited their eggs. Taylor (1912) found that 2 females which were collected May 21 and May 25 in northern Nevada were still carrying eggs.

Desert horned-toads were consistently present in all communities throughout summer but were the least abundant species within the census plots. They had come out of hibernation prior to April 12 and

their relative abundance remained fairly constant from April to August (Fig. 17).

They were never observed up in the shrubs and evidence that they are largely terrestrial in their activities is reflected in an analysis of their stomach contents. More than 55 percent of the total food volume from 16 stomachs consisted of ground beetles and ants (Table 29). Tenebrionids which are slow-moving and largely restricted to the ground were found in 56.3 percent of the stomachs and constituted 32.1 percent of the total food consumed. Ants occurred in all stomachs examined and made up 23.5 percent of the total food volume. As many as 181 ants were found in one stomach. Knowlton (1938) observed a mature horned-toad consume 64 ants within 30 minutes. Small pebbles which had probably been picked up by these lizards in the act of capturing insects occurred in almost half of the stomachs. Seventy-five percent of the specimens were infested with nematodes. As many as 50 nematodes were found in one stomach.

TABLE 29. Stomach contents of 16 specimens of *Phrynosoma platyrhinos* Girard.

	Percent of total volume	Frequency (Percent)
Araneida.....	0.1	6.2
Homoptera.....	0.1	6.2
Hemiptera.....	1.8	25.0
Meloidae.....	0.5	6.2
Coccinellidae.....	1.0	12.5
Tenebrionidae.....	32.1	56.2
Scarabaeidae.....	25.1	100.0
Cureulionidae.....	5.0	12.5
Other Coleoptera.....	2.5	31.3
Coleoptera larvae.....	1.0	12.5
Coleoptera pupae.....	0.5	6.2
Lepidoptera larvae.....	5.2	25.0
Formicidae.....	23.5	100.0
Unidentified insect fragments....	1.6	62.5
Vegetation fragments.....	Trace	25.0
Pebbles.....	....	43.8
Nematodes (parasites).....	....	75.0

Egg-laying had begun during the last part of May and no gravid females were found after the middle of June (Table 26). The number of eggs per female varied from 4 to 9 with an average of 7.1, which is the greatest average number for any of the lizards encountered. The first young horned-toads were seen August 7 in 1939 and July 23, in 1940. These young still retained quite a large quantity of egg yolk within their abdominal cavities and their skin was soft and practically free of spines. Their bodies were also much less dorso-ventrally flattened than the adults.

The low temperatures which prevailed at night inactivated the horned-toads to a much greater degree than some of the other species of lizards. Individuals observed at 5:00 to 6:00 a.m. were almost immobile, even during midsummer. They were most active from 9:00 to 11:00 a.m. and again during the latter part of the afternoon. During midday they

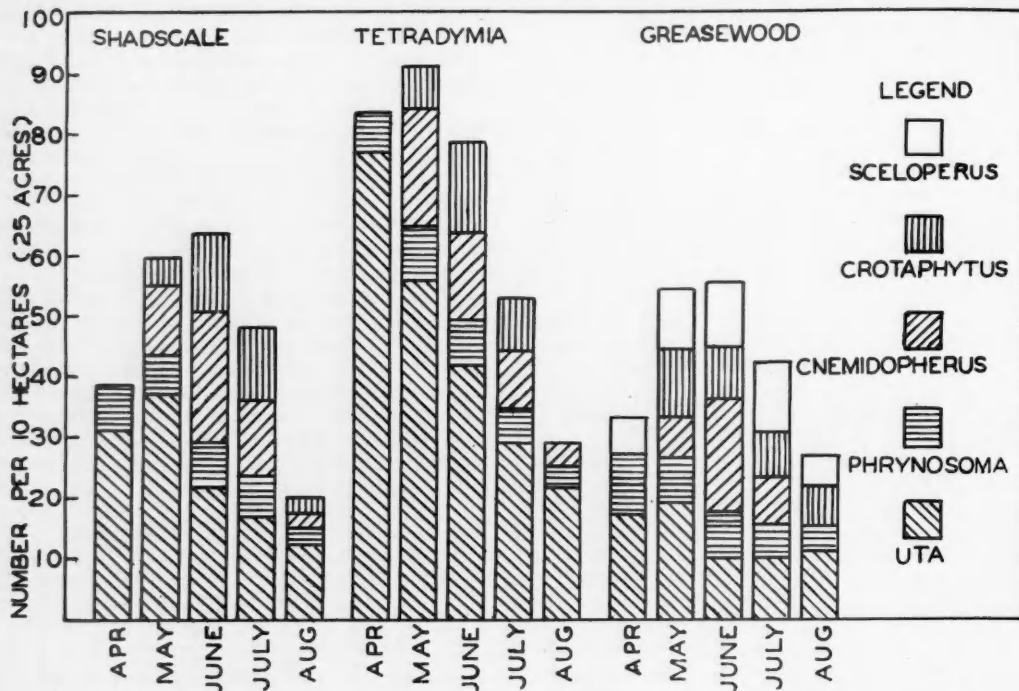


FIG. 17. Seasonal distribution and relative abundance of 5 species of lizards within 3 communities of White Valley, Millard County, Utah.

sought refuge beneath the shrubs or buried themselves in the loose sand. When pursued they attempted to escape beneath shrubs whose lower branches adhered closely to the surface of the ground. When beneath such shrubs they were difficult to extricate because of their posteriorly directed dorsal spines.

The whip-tail lizard is very widely distributed and occurred in all communities but was most abundant in the tetradymia and shadscale (Fig. 17). Their seasonal period of activity was relatively short. None were seen until April 20 and they were not recorded within the census plots until May. They became most abundant in the tetradymia community during late May but reached their maximum in June in the shadscale and greasewood communities. Very few were seen after the first part of August.

They were very rarely seen before 7:00 a.m. and were most active from 9:00 to 11:00 a.m. They usually moved about in a slow, stealthy, jerky manner, especially when they were foraging for food, but when frightened they moved so rapidly that it was sometimes necessary to flush them a second time to make sure of their identity. These sudden bursts of speed were usually of short duration after which the lizard would resume its jerky gait, bobbing its head up and down as it proceeded. Their activities are restricted to the ground as far as could be ascertained. They were seen in the open more frequently

than most other lizards and when pursued they would seek refuge within rodents' burrows more often than beneath the shrubs.

By June 20 only 25 percent of the females were gravid (Table 26). Taylor (1912) observed this species copulating as late as June 10 in northern Nevada and Ruthven & Gaige (1915) report a gravid female being collected July 13 in Elko County, Nevada. The number of eggs per female varied from 5 to 9 with an average of 6.7. The first young whip-tails were seen August 3, 1939 and August 15, 1940. The first young collected varied from 105 mm. to 108 mm. in length and had brilliant bluish-green tails. By the first of September the tails of most of the young had assumed the brownish-grey color of the adults.

The food of this lizard consisted primarily of terrestrial insects but it also fed on insects from low-growing shrubs. Beetles were found in all stomachs examined and constituted more than 20 percent of the total food volume (Table 30). Insect larvae seem to be a favorite food item of this lizard since they comprised almost 50 percent of the total food volume of the stomachs examined. Ants had a low frequency of occurrence and were a minor item of food. Spiders constituted 4.1 percent of the total food volume which is a greater percentage than for any other species of lizard except the uta. Evidence that this species may feed on other small lizards is



TABLE 30. Stomach contents of 10 specimens of *Cnemidophorus tessellatus tessellatus* (Say).

	Percent of total volume	Frequency (Percent)
Araneida.....	4.1	30.0
Acroridae.....	13.4	40.0
Hemiptera.....	5.7	10.0
Tenebrionidae.....	9.0	60.0
Scarabaeidae.....	7.5	10.0
Curculionidae.....	4.5	20.0
Coleoptera larvae.....	18.2	90.0
Coleoptera pupae.....	1.6	10.0
Lepidoptera larvae.....	30.9	70.0
Formicidae.....	0.4	20.0
Other Hymenoptera.....	0.2	10.0
Unidentified insect fragments.....	4.5	70.0

reported by Ruthven & Gaige (1915) who collected a specimen August 14 which contained a recently hatched young of the same species. This lizard was observed feeding on flies and grasshoppers in the field and captive individuals readily ate grasshoppers, flies, and small beetles.

Although the striped racer was found in all communities, it was one of the least abundant snakes encountered. Only 6 individuals were observed and all but one were seen during April, May, and June. The other one was seen during early September. This snake moves very rapidly and was found to prey on lizards and insects. Only 3 stomachs were examined, one of which contained a large whip-tail lizard, another contained 2 utas, and the third one, from a snake only 17 inches in length, contained 2 grasshoppers and 3 tenebrionid beetles. One large racer was observed in the field in the act of trying to capture a whip-tail lizard but the lizard managed to escape. Little is known about the breeding habits of this snake. Woodbury (1931) reports that a gravid female kept in captivity had not deposited her eggs by August 12.

Another snake of minor importance because of its scarcity is the long-nosed snake. One specimen of this species was collected each year within the shad-scale community. One of the snakes was kept in captivity for 7 days during which time it ate 2 utas and several grasshoppers. Tanner (1940) reports only 4 other records of this snake for Utah, all of which are for Washington County in the southwestern corner of the state.

The Great Basin gopher-snake occurred in all communities from the valley floor to the top of the Black Knolls but it was most abundant in the shad-scale community where 54 percent of the total number seen were encountered. This species had emerged from hibernation before the writer's arrival in White Valley in early April. One small specimen, 15 inches in length was collected April 14 and the first adult specimen was seen April 23. Almost 50 percent of the total number seen were encountered during the month of May and 28.6 percent during July (Table 31). This snake is reported to be crepuscular or

nocturnal (Klauber 1939 and Mosauer 1935) but, although the writer spent a considerable amount of time in making observations at night, he found none after dark. Seventy percent of the ones encountered were seen during late afternoon, usually after 6:00 p.m. One individual was collected at 2:30 p.m. after a rainstorm had occurred the night before. They were seen as early as 5:30 a.m. but were never encountered during midday.

The common name "gopher-snake" is very fitting for this species because it preys to a great extent upon ground squirrels which are locally referred to as "gophers." The stomach contents of only 3 specimens were examined but 2 of them contained ground squirrels. One of them had eaten a piute ground squirrel, the second one 2 antelope ground squirrels, and the third one a kangaroo rat. Captive gopher-snakes readily ate kangaroo rats and white-footed mice. As many as 3 mice were eaten by one snake within a period of 28 minutes. Captive snakes which had apparently eaten all that they desired would continue to kill any live mouse or kangaroo rat that was placed in their cages. Woodbury (1928) found a specimen with 9 mice in its stomach and Pack (1919) gives an account of a 3-foot specimen which had eaten 35 small mice.

No data were obtained as to the time of year that this snake reproduces, but according to the observations of Richardson (1915) and Ruthven & Gaige (1915), it must not deposit its eggs until late July or August.

TABLE 31. Frequency of occurrence of gopher-snakes and rattlesnakes from April 12 to August, inclusive.

Months	Percent of total number seen	
	Gopher-snakes	Rattlesnakes
April.....	14.2	0
May.....	47.6	27.8
June.....	4.8	16.7
July.....	28.6	33.3
August.....	4.8	22.2

Rattlesnakes were widespread throughout all communities but were encountered most frequently within the shad-scale and tetradymia communities. They comprised 40.4 percent of the total snakes encountered and 78.9 percent of them occurred within the tetradymia and shad-scale communities.

No rattlesnakes were found before May 6 although a special effort was made to locate them from April 12 up to that time. None had been previously seen by Civilian Conservation Corps personnel or a crew of surveyors who had been working in the field for more than a month before the arrival of the writer. Further evidence that they were just beginning to come out of hibernation about the first of May was obtained from a Civilian Conservation Corps foreman whose men had come into the vicinity of a den on May 7 and had killed 89 rattlesnakes during the day. They were most prevalent during

May and July (Table 31) and after the middle of June they were seen more frequently than gophersnakes. They were still active in early September when the writer's observations were discontinued although their frequency of occurrence was less. All specimens of this species in the Museum of Vertebrate Zoology at the University of California, which have been collected in Nevada, were captured between May 11 and September 9 (Linsdale 1940). These dates agree very well with the observations of the writer, and seem to indicate the limits of the seasonal activity of this species.

Sixty-eight percent of the rattlesnakes were seen after 5:30 p.m. and 27 percent before 9:30 a.m. One was collected at 9:30 p.m. July 11, 1940. This specimen was in the open near a kangaroo rat mound and was presumably seeking food.

Rodents and small birds seem to be their main source of food. The stomach of one specimen contained 2 piute ground squirrels, one of which was partially digested and the other one just recently swallowed. Two others each contained one kangaroo rat, and a fourth one contained a horned lark. One individual was observed to successfully capture a vesper sparrow. Captive rattlesnakes would consume a kangaroo rat every 2 to 3 days, and they would eat freshly killed rats as well as live ones.

The time of reproduction in this species is apparently in late summer or early autumn. Two gravid females were collected May 10 and May 20. The first one contained 12 large ova which had not yet been shed into the uterus and the measurements of which were as follows: (2) 11 x 23 mm.; (2) 12 x 22 mm.; (1) 11 x 22 mm.; (2) 12 x 25 mm.; (2) 13 x 22 mm.; and (3) 12 x 23 mm. The second female contained 8 ova which varied in size from 15 x 32 mm. to 18 x 36 mm. Woodbury (1931) collected a female in August which contained 6 large ova and reports that the young are probably born in the autumn.

## ENVIRONMENTAL RESPONSES OF THE BIOTA

### PLANTS

As has been previously pointed out, the flora of the Northern Desert Shrub Biome is characterized by several species of dominant deciduous shrubs, accompanied by a few dominant grasses and a limited number of subdominant undershrubs and herbs. Eighty-one percent of the plants collected were perennials. Such a predominating percentage seems to reflect a greater survival value of this group in response to the xeric conditions to which they are subjected. Where the production of seed is the only way of insuring the existence of a species from one year to another the chances for its perpetuation are much less due to the possible shortage of sufficient moisture necessary for the maturing of the seed. This hazard was very obvious during the summer of 1940 when many of the plants failed to pro-

duce seed. Flowers were produced but drought prevented the seeds from maturing.

The annuals which do occur, usually reproduce very early in the spring when sufficient moisture is available to complete their life cycle. Many of the perennials, on the other hand, reproduce during the latter part of the summer when the second moist period of the year occurs. This is a rather hazardous time of the year for reproduction because of the variability of the precipitation and only perennials would have much of a chance of survival. During 1940 many of the little rabbitbrush failed to produce flowers because of the lack of moisture during July and August.

All of the dominant grasses are perennials. The only annual grass encountered was the introduced subdominant brome grass which matures its seeds before June. The survival value of grasses is decreased to a lower ebb than for some of the other herbaceous forms due to the coactions of herbivorous animals (both domestic and native) so that the hazards encountered in reproduction are even greater in this group. The capacity to send out new shoots from the more protected basal portion of these perennials is largely responsible for their continued survival under the conditions of heavy grazing and drought to which they have been subjected.

The dominant shrubs seem to have acquired their distinctive life-form in response to the arid climate to which they have been subjected. They all belong to herbaceous families which have acquired shrubby adaptations and are not dwarfed forms of larger shrubs and trees such as occur in the chaparral or alpine communities. Two species of ephedra were the only shrubby components encountered which did not belong to either the aster family (Asteraceae) or the goosefoot family (Chenopodiaceae). These two families comprised 49 percent of the total species identified and are all perennials except the Russian thistle, which is an introduced species. This shrubby life form makes possible the attainment of larger sized plants, by small increments of growth each year, than could be attained during the short period of time when sufficient moisture is available, if the entire plants were reproduced each year.

Two types of root systems are very characteristic of these xerophytic plants. The one is a long taproot which makes possible the utilization of deep soil moisture and the other is a widely branched system of roots near the surface which facilitates the rapid utilization of the limited amounts of periodic precipitation.

In response to the limited amount of available moisture, most of the plants are widely spaced, grow very slowly, are rather small, and cover only a small percentage of the area on which they occur. Such plants have been termed "drought evading plants" (Shantz 1927), because they evade early desiccation by delaying the eventual exhaustion of the available soil moisture through the above adaptations. Such spatial relations are not only character-

istic of the shrubs but occur in most of the dominant grasses.

Conservation of water and the prevention of excessive water losses from transpiration is accomplished through morphological adaptations such as reduction in leaf surfaces, heavy cutinization of the epidermis, extreme pubescence of leaf surfaces, and the shedding of leaves. Bud sage and tetradymia shed practically all of their leaves very early in the summer and go into an apparent state of dormancy, appearing as if they were practically dead. The leaf surfaces of shadscale, winterfat, and sagebrush are relatively small and are so pubescent that these plants are gray to almost white in color. The leaf surface of the greasewood, suaeda, and gray molly is reduced by their linear proportions and the leaves of the greasewood are so heavily cutinized as to appear as if they were glazed. The ephedra and pickleweed leaves are reduced to mere scales and the stems function in photosynthesis. During extreme conditions of drought the transpiration surface of the ephedra plants is often reduced by the shedding of parts of the stems.

Physiological adaptations such as increased osmotic pressure values of the cell sap have been developed by many of the plants, thus enabling them to obtain moisture from the soil where moisture equivalent values are low or where the mineral content of the soil is high (Shantz 1916, Harris, J. H. *et al.* 1924). These studies show that the osmotic concentration of the cell sap of the dominant plants from different communities is inversely proportional to the available moisture. The cell sap of sagebrush, which grows where the greatest amount of moisture is available, has been found to have an average osmotic value of about 22 atmospheres whereas the cell sap of shadscale averages 43.6 atmospheres and sometimes exceeds 150 atmospheres where the moisture supply is lowest. Greasewood, growing in situations where underground water is available but where the salt content of the soil is apt to be higher, has a cell sap osmotic concentration intermediate between the above two, averaging about 30 atmospheres (Harris, J. A. *et al.* 1924). This correlation between osmotic concentration of plant tissue fluids and the availability of moisture has been further demonstrated by comparisons between the shrubs and the ephemeral herbs, always being considerably lower in the herbs which occur at the time of the year when the greatest amount of moisture is available.

#### MAMMALS

The survival value of any organism is dependent on its physiological and morphological adaptation to the environmental conditions to which it is subjected or to its ability to escape those conditions not favorable to its existence. The first type of response is more characteristic of plants because of their lack of motility and is manifest by morphological changes in life form and physiological adaptations such as have been described. Morphological and physiologi-

cal adaptations also occur in animals but they are greatly augmented by adaptive types of behavior which enable them to evade the critical environmental extremes to which they are subjected.

The mammals in general are light in color in keeping with the general light tone of the sparse vegetation and the soil. Correlations between the pelage color of many different rodents and the color of the soil has been frequently observed in areas of sparse vegetation in southwestern Utah (Hardy, 1945) and in other parts of southwestern United States (Benson 1933, Dice and Blossom 1937, and Hooper 1941). Natural selection, resulting in the elimination of those individuals which do not blend into their backgrounds is thought to be an important factor responsible for such correlations (Benson 1933, and Dice and Blossom, 1937), but this protective coloration theory is discredited by others (Buxton, 1923, and Summer 1921 and 1925). As yet there is little experimental evidence as to what the causes may be. High temperatures and low humidities, which are often postulated to be responsible for pallid coloration, have been found to induce no detectable changes in various species when reared under controlled conditions for as many as twelve generations (Summer 1924).

Most mammals of the communities studied escape the hot summer temperatures by remaining under ground during the day. The high air and soil surface temperatures are not transmitted very far beneath the surface of the ground and relatively moderate and constant temperatures are quickly reached, as has been clearly shown by Vorhies (1945). The data presented in Table 32, compiled from Sinclair (1922), also shows that within a relatively short distance beneath the surface of the soil the temperatures are much lower and that the daily range in temperature at a depth of only 10 centimeters is less than one-eighth as great as at the surface.

TABLE 32. Soil temperature. From Sinclair, 1922. June 21, 1915 at Tucson, Arizona.

	Maximum °C	Time	Minimum °C	Time	Daily Range °C
Shelter.....	42.5	1:00 p.m.	11.0	4-5 a.m.	31.5
Soil 0.4 cm..	71.5	1:00 p.m.	15.0	4-5 a.m.	56.5
" 7.0 "	44.1	4:30 p.m.	25.2	6:00 a.m.	18.9
" 10.0 "	40.1	6:00 p.m.	26.3	6:30 a.m.	13.8
" 20.0 "	33.4	9:00 p.m.	29.0	10:30 a.m.	4.4
" 30.0 "	29.8	10:30 p.m.	27.8	12:00 n	2.0
" 45.0 "	27.9	10:00 a.m.	27.8	2:00 p.m.	0.1

Sixty-eight percent of the mammals encountered were nocturnal. When the rodents are considered separately this response was even more striking, the percentages being 79 nocturnal and 21 diurnal. Although the diurnal species were active to a certain extent throughout the day yet there was a decrease in their activity during the midday hours. One diurnal species, the piute ground squirrel evades late summer high temperatures by aestivating. It remains within its burrow from July until the fol-

lowing February or March. The fact that the antelope ground squirrel remained active throughout the summer suggests the possibility of certain physiological differences and/or differences in the diets of these two species which are responsible for this difference in seasonal behavior.

Although the rabbits are crepuscular and nocturnal they remain above ground where they are exposed to the normal air temperatures throughout the day. They leave the more open areas during midday and go into areas where the tallest vegetation occurs and consequently where there is the greatest amount of shade. During the heat of the day they remain relatively inactive within their forms which were found to be almost invariably situated in the north and east sides of the shrubs where the maximum amount of shade is obtained during the hottest part of the day.

Temperature does not only alter the behavior of diurnal animals but it also has a pronounced effect on the time of activity of nocturnal species. Their time of activity tends to be progressively delayed until later hours of the night as the daily summer temperatures increase. During each month a limited number of trapping plots were visited every 2 hours during the night and the number of rodents caught was recorded. During May about 80 percent of the kangaroo rats were caught before 11:00 p.m., 32 percent of them being caught before 9:00 p.m. During July and August only 32 percent of them were caught before 11:00 p.m. The air temperatures most favorable for the activity of these rodents were apparently between 55° to 75° F., since that was the general range at which the greatest number were caught regardless of time of night or time of the season (Table 33).

TABLE 33. Kangaroo rat activity as indicated by number caught at different times of the night on 10 different plots from May to August, 1940.

Dates	Before 9:00 p.m.			9:00 to 11:00 p.m.			11:00 p.m. to 1:00 a.m.			After 1:00 a.m.		
	Temperature °F.	Number	Percent of Total	Temperature °F.	Number	Percent of Total	Temperature °F.	Number	Percent of Total	Temperature °F.	Number	Percent of Total
May 21.....	58	1	25	56	2	50	53	1	25	49	0	0
" 21.....	58	2	22	56	7	78	53	0	0	49	0	0
" 26.....	55	6	43	52	5	36	50	2	14	46	1	7
June 11.....	67	1	25	68	0	0	58	2	50	53	1	25
" 11.....	67	0	0	68	0	0	58	4	80	53	1	20
" 28.....	79	0	0	75	0	0	72	3	100	55	0	0
" 28.....	79	0	0	75	0	0	72	0	0	65	2	100
July 17.....	77	0	0	75	4	36	74	0	0	64	7	64
Aug. 11.....	79	0	0	76	0	0	73	0	0	60	4	100
" 11.....	79	0	0	76	0	0	73	0	0	60	3	100

The ability of mammals from arid regions to dispense with the ingestion of free water has caused considerable speculation but has received little scientific investigation and the role of metabolic water in desert animals has been grossly over-estimated.

Since metabolic water is produced solely by the oxidation of proteins, fats, and carbohydrates, desert animals can presumably produce no more than aquatic ones. This metabolic water may be sufficient in certain insects and small rodents to meet their physiological needs but in most of the larger mammals it must be supplemented by free water. During the winter the problem is less serious because snow remains on the ground for considerable periods and can be utilized. Water losses from the surface of the body are also less during that time of the year due to lower temperatures and increased relative humidity. More metabolic water may also be available due to increased rates of metabolism for heat production. During the summer months just the converse is true. Less free water is available, water losses from the body are apt to be higher and the production of metabolic water lower. A certain amount of water is obtained from succulent plants by some mammals such as ground squirrels and rabbits and some from animal food by certain carnivorous species, but in the case of animals as large as the antelope and the coyote this supply is inadequate and must be supplemented by available sources of drinking water. Barnes (1929) postulates that the antelope may be able to persist without drinking water but such a hypothesis is very doubtful. Even in winter when snow is available antelopes usually seek out watering places about every four days (Rouse 1941). Although antelopes are often seen 40 to 50 miles from any known water supply they move very rapidly and can get to a water supply within a short time. There may also be seepages and small springs within their range which are unknown to man. Natural cavities in rocks filled with rainwater may also serve as a supply of drinking water for several weeks.

Many of the mammals are able to persist on the small quantities of water principally by conservation of the supply within their bodies. Most of the small rodents such as pocket mice, kangaroo mice and kangaroo rats feed on air-dry plant seeds and leaves and apparently persist almost entirely on metabolic water. Similar observations have been made on various species of Heteromyidae in other arid regions (Stephens 1906, Vorhies and Taylor 1922, Hall and Linsdale 1939, and Hawbecker 1940). Those factors which increase the rate of metabolic water production or conserve water within the body are of primary importance to animals in arid regions. Since an increase in the production of metabolic water necessitates an increase in the rate of metabolism it might appear as if an increased metabolic rate might be advantageous and characteristic of desert animals. However, factors directly concerned with increased rates of metabolism include increased rates of respiration, body temperature, and general activity. It is quite obvious that an increase in any one of these, to produce more metabolic water, would also increase the water loss from the body, and a vicious cycle would result. Evidence seems to indicate that on the whole the greatest economy of water is at-



tained by animals kept on a dry diet where the rate of metabolism is lower and where the activity of the animal is reduced (Howell and Gersh 1935). Although metabolic water is very important, its increase to any appreciable degree through increased activity of the animal seems to be too expensive, by way of water losses, to be practical.

Diet is one factor which would seem to be of great importance in the water economy of mammals. Inasmuch as the end product of protein metabolism is urea, which is soluble and necessitates the presence of considerable amounts of water for its elimination, it would appear that desert animals would fare better on a diet low in nitrogenous constituents. Since carbohydrates will furnish approximately 55% of their weight (more or less in accordance with their hydrogen content) in metabolic water and fats more than their own weight, a diet high in these two constituents would be to the advantage of the desert mammals. Burr & Burr (1930) found that white rats on a fat-free diet required twice as much water as rats furnished 10 drops of lard per day, although the excess water was not eliminated through the kidneys. Vorhies (1945) reports a striking correlation between the food habits of several different species of rodents and the microclimates of their habitats. Those species, such as the kangaroo rat, which obtain practically no free water from the foods they consume, are strictly nocturnal and spend most of their time within a microclimate of their burrows which is less conducive to water losses from the body. Other species, such as the jack rabbit, which are subjected to environmental conditions conducive to greater degrees of desiccation, obtain sufficient water by feeding on more succulent plants.

Any factor which will reduce the rate of respiration and loss of water from the surface of the body would be of a distinct advantage to mammals in arid regions. Thus most of the rodents of such areas are active during only a small part of the day and at a time when it is coolest and the evaporating power of the air is lowest. During the hot part of the day they remain within their burrows where it is cool and where the underground moisture is not dissipated so rapidly. The work of Howell and Gersh (1935) suggests that the dry diet of kangaroo rats is conducive to lower respiratory rates and consequently to a reduction in water losses.

Secretions from oil glands of the kangaroo rats are very conspicuous and may play a part in preventing water losses from the surfaces of the body. When deprived of a sand bath the pelage of these animals assumes an oily and unkempt appearance within two or three days.

The feces of desert animals are very dry indicating an efficient reabsorption of water within the large intestines. Howell & Gersh (1935) have shown that water in the urine may be conserved for reutilization by kangaroo rats fed on dry diets through physiological means of reabsorption common to the kidney of other mammals, but supplemented by a marked increase in the reabsorptive powers of the

large ducts of the renal papilla, and by a reabsorption of water in the bladder. This mechanism for water conservation and reutilization was exhibited only in kangaroo rats fed on dry diets and seems to be an adaptation that is peculiar to mammals living under arid conditions.

#### BIRDS

Many birds of the Great Basin have certain morphological and structural characteristics which serve to distinguish them from other birds, of even the same species, in other parts of the United States. Most of them are characterized by plain pallid colors which not only serve to reflect the sun's rays but also blend in with the general light colored soil and sparse vegetation thus affording protection where an adequate vegetation screen is lacking. Linsdale (1936) found a high positive correlation between the lining of the nests and coloration of nestling plumages (down) with the vegetation cover at the nest site and the general climatic ranges of the birds. The light colored plumage of the nestlings and adult birds may be the result of natural selection but the light colored nest linings appears to be largely a circumstantial matter. The materials used in lining the nests are usually dried grasses and light-colored vegetation fibers which are the most available materials for building nests in the communities concerned. Wool, which would not be present under natural conditions, was frequently found lining nests because it was readily accessible and apparently not because of any predilection on the part of the birds.

The nests of practically all species were placed on or near the surface of the ground due to the small size of the plants and most of them were located on the east or northeast side of the plants (Table 20). Such a position affords the greatest possible amount of protection from the sun during the hot afternoon hours and affords warmth during early morning hours which are usually chilly in such regions. Linsdale (1938) reports this same phenomenon in Nevada and attributes it to preferences on the part of the birds for the warmest side of the shrubs during the early morning hours when the nests are being constructed.

Long-range vision is very noticeable and is probably an important factor in the protection and social relations of these birds where the low-growing plants afford little protective cover and where the birds tend to be widely separated. This scattered distribution also necessitates a high development of the vocal powers in order that the birds may hear one another. Birds of central Nevada have been found to have much louder voices than those of the same species along the Pacific coast (Linsdale 1938a).

The flight of most species is very rapid and all species of passerine birds except the horned lark tend to fly low, seemingly to be within the protection of the low shrubs. This low-flying characteristic may not only be a means of evading enemies but it is also a means of evading the strong winds which are so prevalent in the area. Even ravens were ob-

served to fly very low during strong winds and follow along ravines below the general level of the terrain.

The high temperatures are tolerated principally by seeking shade within the largest shrubs. Bird populations were higher in the greasewoods during the hotter part of the day than in the mornings and evenings because the birds coming in from the more open adjacent areas sought the shade of the larger greasewood shrubs during midday. In the open shade and tetradymia communities the bird populations decreased considerably after the nesting season when summer temperatures reached their maxima.

The lack of sweat glands in birds helps to prevent losses of water from their body surfaces. Water is also conserved by the excretion of nitrogenous waste materials in the form of semi-solid uric acid. When the end product of excretion is uric acid, approximately 53% of metabolic water has been found to be obtainable from nitrogenous oxidation, while with urea only 42% is thus obtainable (Howell and Gersh 1935).

#### REPTILES

Although reptiles are very characteristic of arid areas where temperatures often become high, they have few physiological adaptations which better enable them to withstand the high temperatures of such areas than mammals and birds. In fact their poikilothermic characteristics may be a handicap where daily and seasonal fluctuations in temperature are as great as they are in western Utah. Their seasonal and daily periods of activity are very short being affected by both high and low temperatures. Being so closely associated with the ground they are subjected to an environment where temperatures get much higher than the air temperatures and often reach 130° to 140° F. Experimental evidence indicates that most reptiles will succumb to such temperatures if exposed for only a few minutes and that diurnal species are no more heat-tolerant than nocturnal ones (Mosauer 1936). Most reptiles have been found to register marked discomfort at temperatures 5° F. above their optimum and exposure to higher temperatures causes death from a minute to an hour, the time element depending on the ground temperature, intensity of radiating capacity for color change and volume of the reptile. Cowles (1939) postulates the possibility of high temperatures and increased insolation, rather than cold, as being the chief element responsible for the disappearance of the Mesozoic reptilian fauna. The present day reptiles are able to persist only by altering their behavior so that they are not exposed to the daily temperature extremes. Lizards have an advantage over snakes because their body is elevated somewhat above the ground and their mode of locomotion enables them to move more quickly from one bit of cover to another.

The chromatophores of the skin function to a certain extent in thermo-regulation in reptiles but the

degree of its effectiveness is not very great. The pigment cells are stimulated by both temperature and light with temperature being of primary importance. At low temperatures the melanophores expand and the skin is darkened thus facilitating a maximum amount of heat absorption and making it possible for the reptile to become active earlier in the day. At higher temperatures the melanophores contract causing the skin to become light and absorb less heat from the sun, thus extending the length of the reptiles' daily period of activity. The critical temperature for inducing the light phase in most iguanids is about 95° to 110° F. but may be as low as 77° F. in the *uta* (Atsatt 1939). In correlation with this experimental reaction of the *uta*, the writer found that this species became active much earlier in the morning than any other species of lizard. It was often active before 6:00 a.m. during the midsummer. Horned-toads encountered at such time of the day were practically immobile.

Since this thermo-regulator mechanism is of little use above the point where a maximum degree of blanching is induced, it is necessary for these animals to avoid the lethal daily temperatures by crawling into burrows, burrowing in the loose soil, and seeking shelter beneath rocks and vegetation. This evading reaction is very well reflected in the decreasing number of reptiles seen as the summer temperatures increased (Fig. 17).

Reptiles are morphologically and physiologically well adapted for water conservation which is very important to animals living in arid regions. Water losses from the body surfaces is reduced to a minimum in this group by their impervious integument and by very little water being excreted. The feces are eliminated as a dry mass containing practically no water and the urine is composed of an equally dry mass of uric acid and its salts which are insoluble and can be excreted in a solid form (Weese, 1917). These adaptations enable them to exist without the ingestion of free water. Their entire water requirements are met by the water contained in their food and by water which is produced as a result of the metabolic processes of the body. This protection against water loss is so effective that the reaction of the horned-toad in a gradient of the evaporating power of air has been found to be very indifferent unless the gradient is extremely steep (Weese, 1919a).

#### INVERTEBRATES

The responses of the invertebrates to environmental factors was not as apparent as they were in the vertebrates but some rather detailed observations were made on a few of the more common species. Since ants were very abundant and exhibit very diversified habits, they were of particular interest. Among this group are both diurnal and nocturnal species. The harvester ant, a very widely distributed diurnal species, seems to be able to withstand much higher temperatures than many other species of ants, especially the honey ant, *Myrmecocystus mexicanus*



FIG. 18. Cone-shaped mound of the honey ant (*Myrmecocystus mexicanus navajo*) within the shadeless community. (July 14, 1940.)

*navajo* Whlr. which is crepuscular or nocturnal. The harvester ants emerged from their mounds about 7:30 a.m. during midsummer and were inactive only when the air temperatures exceeded 90° F.

The honey ant builds a funnel-shaped mound of small pebbles with an opening at the bottom of the funnel leading to a labyrinth of galleries extending 2 to 3 feet below the surface of the soil (Fig. 18). By remaining within these galleries they are able to avoid the high outside temperatures which they are unable to tolerate. When exposed to the direct rays of the sun at a temperature of 94° F. these ants were killed within 1 to 10 minutes. Their sensitivity to temperature was very markedly reflected in the time of their activity at different times of the year. During April they became active just before dark and the time of their activity was progressively delayed until a later hour of the night as the summer temperatures became higher. By midsummer they failed to emerge until near midnight. Observations were made on the time of emergence of these ants from their mounds at frequent intervals from April 19 to September 2, during which periods the position of the ants were recorded every 3 to 15 minutes

and any significant changes in their position were recorded at the time that such changes occurred.

In presenting the data obtained from those observations the writer finds it convenient to divide the progress of the emergence of the ants from their mound into 3 stages. The first stage is the first appearance of the ants below the aperture of the funnel; the second stage, the occurrence of the ants above the aperture, but still remaining well toward the bottom of the funnel; and the third stage, their actual leaving of the mound.

As the season progressed and the daily temperatures became higher there was a definite tendency for the ants to delay the time of their emergence. The correlation between the time of their leaving the mound and the daily mean temperature during midsummer is not too close, the increased delay in the time of their leaving the burrow being much greater in proportion to the increase in daily mean temperature at that time than it had been earlier in the season (Fig. 19). Unfortunately the soil temperatures were not recorded and it may be that the ants were responding to the surface soil temperatures rather than to air temperatures. Since the surface soil temperatures rise considerably higher than the air temperatures during the day and drop more slowly during the night this may account for the longer delay of these ants in leaving their mounds during midsummer.

The air temperatures at which the ants first appeared below the aperture of the funnel varied from 58° F. to 88° F. with an average of 68° F. for the entire period of investigation. The air temperatures at the time they were in the bottom of the funnel varied from 56.4° F. to 83.5° F. with an average of 66.6° F. The air temperatures at the time they left the mound ranged from 52.2° F. to 70.5° F. with an average of 63.5° F.

There was a considerable variation in the length of the 3 different designated stages at different times of the summer. The range in the time of their appearance below the aperture of the funnel amounted to 2 hours and 12 minutes; the time of their aggregation above the aperture of the funnel was 2 hours and 36 minutes; whereas the range of the time of their leaving the mound amounted to 4 hours and 34 minutes. Thus the length of time the ants remained at each of the designated points varied at different times during the summer. From April 18 to the last part of May, when the daily mean temperatures did not rise above 70° F., the interval from the time the ants first appeared below the aperture until they left the mound ranged from 12 to 40 minutes with an average of 31 minutes. From the first part of August until September 2 the range was from 1 hour and 22 minutes to 1 hour and 25 minutes with an average of 1 hour and 23 minutes. During the early part of the summer the ants left their mound soon after emerging into the base of the funnel, the average time, up to the last of May being 15 minutes with a range of 6 to 24 minutes. During midsummer they remained within

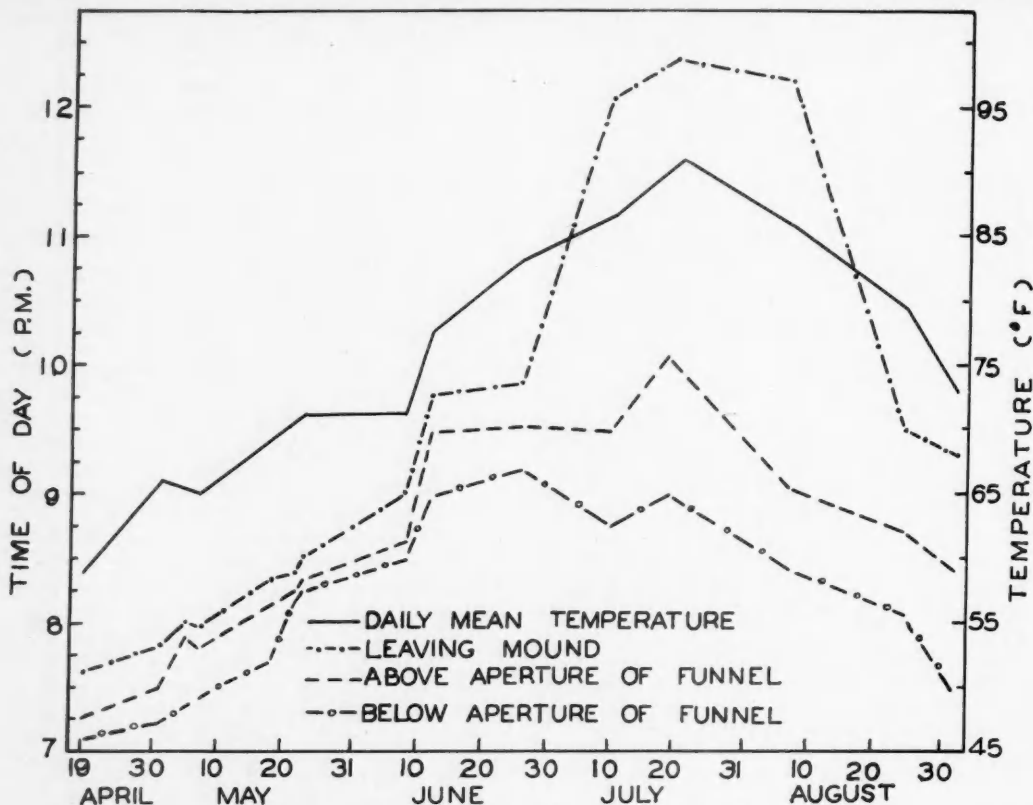


FIG. 19. Activity of the honey ant (*Myrmecocystus mexicanus navajo*) in relation to daily mean temperatures.

the funnel for 16 minutes to 2 hours and 44 minutes with an average of 1 hour and 25 minutes while during the latter part of the season they remained within the funnel only 51 minutes.

A great many species of invertebrates are strictly nocturnal and escape the high temperatures during the day by remaining in burrows or beneath rocks and vegetation. The large tenebrionid beetles were both diurnal and nocturnal but were most active during the cooler hours of the day. Such diurnal species as grasshoppers were usually found during the hottest part of the day on the shady side of the plants and oriented along the longitudinal axis of the stems parallel with the rays of the sun.

Water losses in insects are reduced to a minimum by their chitinous exoskeleton and by the excretion of a dry urine in which uric acid is the sole nitrogenous constituent. The large black tenebrionids which are so characteristic of the communities studied are particularly well protected against water loss. Their elytra is fused together forming a very impervious armor. Experiments by Weese (1919) indicate that these insects lose little or no water from their body surfaces since they exhibit no definite re-

action to either low or high relative humidities when subjected to a gradient ranging from 6 to 98%.

The water supply of insects is obtained from the food they ingest and from physiological metabolic processes. Certain tenebrionids are known to live throughout their natural lives without any inhibition of water (Babeock 1912).

#### SUMMARY

Many of the plant communities of western Utah have received a considerable amount of attention because of their significance as indicators of soil conditions in relation to the economic pursuits of man, but no previous attempt has been made to investigate the total biotic components and analyze their bio-ecological relationships. This study was undertaken for that purpose and an attempt was made to investigate the biotic constituents from the standpoint of their distribution, relative abundance, interactions and environmental responses.

The shadscale association and its related communities were studied in White Valley which is located in Millard County, 65 miles west of Delta, Utah. The sagebrush community was studied in Fernow



Valley located about 15 miles west of Levan, Utah in the eastern part of Juab County.

Field observations were made from June to September, 1939 and from April to September, 1940. Quantitative methods were employed in studying both the plants and animals of the various communities, supplemented by general cruising observations. The principal plant components for each community were calculated in terms of percent of the total floral composition, frequency of occurrence in quadrat samples taken, and percent of the total ground surface covered. One square meter samples of the invertebrate populations were taken every 7 to 10 days by making 50 sweeps with an insect net 30 centimeters in diameter. The frequency with which the larger vertebrates were seen or heard, together with the frequency with which their "signs" in the form of scat, tracks, and dens or nests were encountered, were used as indices of their relative abundance. Estimates of the bird and rabbit populations were made by counting the number of individuals within 4-hectare (10-acre) sample plots. The relative abundance of the smaller rodents was determined by trapping 0.4-hectare (1-acre) and 0.2-hectare (0.5-acre) plots for 4 consecutive nights. The relative abundance of lizards was estimated by making counts within the same plots that were utilized for trapping rodents. Daily records of temperature, relative humidity and evaporation which were kept while the field work was in progress were supplemented by climatic data from government weather stations located within shadscale and sagebrush areas throughout western Utah.

The biotic communities of the Great Basin region occurring at elevations below the piñon-juniper woodland and extending from the Palouse prairie areas of southern Idaho and southeastern Washington to about 37 degrees south latitude, where they merge in the Southern Desert Scrub Biome in southern Utah, are designated as constituting the Northern Desert Shrub Biome. The term "Northern" is used to denote a semi-desert climate and to differentiate it from the more arid desert of southwestern United States. The "Atriplex-Artemisia Association" of Clements is divided into two separate associations, sagebrush and shadscale, on the basis of differences in available moisture, distribution of the dominant plants and composition of the various biotic components.

The sagebrush community occurs along the windward bases of mountains or in valleys where the precipitation is greater and/or where the soil is deep, more permeable, and relatively saline-free, whereas the shadscale and its closely related communities occupy the more xeric areas where the soil is often impregnated with mineral salts. Temperature conditions are very similar in both associations ranging from a maximum of 115° F. to a minimum of -28° F. with an annual mean of 49.9° F. in the sagebrush areas, as compared with a maximum of 110° F. to a minimum of -30° F. with an annual mean of 49.5° F. in the shadscale areas. Annual precipitation is about 100 percent greater in the sagebrush

area than in shadscale areas, with an average of 14.84 inches in the former as compared with 7.95 inches in the latter. The distribution of the precipitation throughout the year is much the same for both associations and most of it occurs in the form of snow. June is the driest month of the year although very little precipitation may fall during July in some years.

Considerable variation occurs in the composition of the shadscale association with the result that a number of distinct edaphic biotic communities, designated as faciations, were differentiated on the basis of the deletion or addition of one or more dominants. These variations seem to be the result of differences in the availability of soil moisture which is altered by the texture and mineral content of the soil.

The shadscale, tetradymia, greasewood, and sagebrush communities were studied most intensively and are described in greatest detail. The plants and invertebrates are regarded as constituting the biotic matrix of the various communities. The relationships of the vertebrate animals to the biotic matrix, together with their interactions and environmental responses, are described as far as they are understood.

Each community is characterized by rather sharp boundaries, by one or two rather widely spaced dominant deciduous shrubs, accompanied by several dominant grasses, and a limited number of subdominant under-shrubs and herbs. Except for a small portion of the lowest part of the valley floor in White Valley, which consists of a barren playa, so heavily impregnated with mineral salts that no plant life can exist and which is fringed in some places by a border of pickleweed, the greater part of the floor is occupied by the greasewood faciacion. As this community extends towards the outer edges of the valley floor, shadscale becomes increasingly abundant and in some places an ecotone is formed between the two communities. The shadscale association extends from the upper border of the valley floor toward the base of the mountains and occupies a much greater part of White Valley than any other community. The principal dominants of this community include shadscale, winterfat, bud sage, Indian rice grass, and galleta grass. As this community approached the base of the mountains a new dominant *Tetradymia glabrata* became very prevalent in some areas. The tetradymia faciacion thus occurred as a discontinuous narrow band at the base of the mountains where the soil was coarse in texture, well-drained and where there were usually many large boulders. The winterfat faciacion was also edaphic in nature and often occurred as "islands" within the shadscale community where the soil was sandy. This community has probably been greatly reduced in extent by the grazing of domestic animals because winterfat, the principal dominant, is utilized to a great extent as forage for sheep. The black sage community occurred on a series of black lava rock knolls where the soil was shallow and very coarse

in texture. The subdominant little rabbitbrush was very widespread and in some areas where the soil was very shallow or where the characteristic dominant shrubs had been disturbed or depleted, it formed a developmental community (associates) of considerable extent.

Arachnids, tenebrionid beetles and ants were very prevalent and conspicuous members of the ground society in most communities. The invertebrates of the dominant shrubs varied greatly in abundance and species from one community to another. They were consistently most abundant in the sagebrush and greasewood communities and least abundant in the shadscale. Maximum invertebrate populations occurred during the month of May in all communities except the greasewood, after which they declined as the summer temperatures increased. Invertebrate populations of the greasewood community remained fairly constant during midsummer and reached a maximum about the middle of June when populations of other communities were beginning to decline. The greatest fluctuation occurred in the tetrady mia community where the dominant plants produced profuse inflorescences that attracted numerous small hemiptera during early May. Following a very high population level, which exceeded that of any other community during May, the abundance of insects declined very rapidly as the tetrady mia matured its seeds and shed most of its leaves in response to the xeric conditions to which it was subjected.

Most of the major influent mammals, such as the badger, coyote, and antelope ranged throughout all communities. Although continuous predator control measures are exerted against the coyote by stockmen and government agencies, it continues to be very prevalent and was the most ecologically important major influent in all communities. It was most abundant in the greasewood and sagebrush communities where there was the greatest amount of cover and where its basic food supply (rabbits) was most abundant. Its coactions are far-reaching because it is active throughout the year and because it feeds on such a variety of biotic components from insects to the largest mammals. The badger has been greatly reduced in numbers through the predator control activities of man but it still is an important major influent because it feeds on many of the prevalent rodents and because its burrows are utilized by so many other species of animals such as the burrowing owl, cottontail rabbits, foxes, coyotes, and many of the smaller animals of the community. The distribution of the burrowing owl seemed to be practically dependent on badger excavations.

The major influent birds also ranged throughout all communities. The most important species observed included the Swainson hawk, marsh hawk, prairie falcon, and the burrowing owl. The burrowing owl was most prevalent in the shadscale community. So pronounced were the effects of this owl within the community that rodent populations within the vicinity of its burrows were practically nil.

The smaller vertebrates were much more numerous and although many of them occurred in all the biotic communities they varied in abundance from one community to another. Heteromyidae, consisting of 3 species of pocket mice, 2 of kangaroo rats, and one kangaroo mouse, were very prevalent throughout all communities. *Perognathus parvus* was restricted to the sagebrush community; *Perognathus formosus* occurred only in the black sage and tetrady mia communities; and *Perognathus longimembris* was most prevalent in the shadscale community. *Dipodomys microps* occurred in all communities, but was most abundant in the shadscale and tetrady mia communities where it constituted 80.6 and 60.9 percent respectively of the total rodent populations. *Dipodomys ordii* occurred in all communities except the black sage and was more abundant than *D. microps* in the greasewood and sagebrush communities. The kangaroo mouse occurred in several communities of White Valley but was never abundant, being most prevalent in the winterfat community. The piute ground squirrel was most prevalent in the vicinity of Tule Springs in the greasewood community and in the sagebrush community whereas the antelope ground squirrel was most prevalent in the shadscale community. Chipmunks were never abundant and occurred only in the sagebrush community. The pocket gopher occurred in most communities except where the soil was shallow and rocky but it was never abundant, being most prevalent in the greasewood community in the vicinity of Tule Springs. The number of grasshopper mice trapped was very low, although this species occurred in most of the communities of White Valley. The harvest mouse occurred only in the greasewood, shadscale-greasewood ecotone, and sagebrush community, being most prevalent in the greasewoods. *Peromyscus maniculatus* occurred in all communities but was largely replaced by an ecological equivalent, *Peromyscus crinitus*, in the black sage community, the latter species being restricted to the black sage. The pack rat was present only in the black sage and tetrady mia communities where large boulders and cliffs provided adequate sites for its dens. Jack rabbits were widespread but were most abundant in the greasewood and sagebrush communities. Cottontail rabbits were largely restricted to the tetrady mia and black-sage communities where large rocks and ravines were present.

Passerine bird populations were low and the resident species few in number. Populations were highest in April and May in the shadscale and tetrady mia communities and in August in the greasewood community.

Reptiles were very conspicuous minor influents from April to August but their ecological importance is limited by their short seasonal period of activity. This group consisted of 6 species of lizards and 4 species of snakes. The brown-shouldered uta was not only the most abundant lizard but it had the longest daily and seasonal periods of activity and occurred in all communities, being most numerous

in the tetradymia community during April and May. The collared lizard was restricted to the tetradymia and blacksage communities, whereas the sagebrush lizard occurred only in the sagebrush and greasewood communities. All other lizards occurred in most of the communities but they varied in abundance from one community to another. The utas began depositing their eggs soon after the middle of April and had completed their egg-laying activities in early June when most of the other lizards were just beginning to lay their eggs. The food of most lizards consisted primarily of insects. Terrestrial insects, such as ants and ground beetles, constituted the greater part of the diet of the strictly terrestrial species such as utas and horned-toads, whereas homoptera and hemiptera were most frequently eaten by the shrub-inhabiting sagebrush lizard. The leopard-lizard and collared lizard were found to be carnivorous as well as insectivorous and fed to a considerable extent on utas. The gopher-snake and rattlesnake were the most prevalent snakes and both were most abundant in the shadscale and tetradymia communities. Gopher-snakes were encountered almost a month earlier than rattlesnakes but both species were most prevalent during May and late July.

Soil texture seemed to be a very important factor in the determination of the distribution of many of the biotic components. It not only influenced the composition of the plant life but also had a pronounced effect on the distribution of many of the animals. The kangaroo mouse and one species of kangaroo rat (*Dipodomys ordii*) were most frequently encountered in areas of fine gravel and sandy soils, whereas *Dipodomys microps* and *Peromyscus crinitus* were most abundant where the soil was very coarse in texture. The brown-shouldered uta was most abundant in the tetradymia community where the soil consisted principally of coarse gravel, whereas the leopard-lizard was most prevalent in sandy areas. The pack rat, long-tailed pocket mouse (*Perognathus formosus*), rock wren, and the collared lizard were restricted to those communities where the soil was very rocky and where there was an abundance of large boulders.

The height, density, and general vegetative form of the dominant plants also influences the composition of many of the biotic communities. The dominants of the greasewood and sagebrush communities are very similar in vegetative form, height, and density and many of the vertebrate components of these communities were more nearly alike, although the communities studied were more than 100 miles apart, than were the components of the greasewood and shadscale communities which were adjacent to each other in White Valley. Coyotes and jack rabbits were much more prevalent within the greasewood and sagebrush communities than in any other. The harvest mouse and sagebrush lizard were never encountered elsewhere; and the shrike, sage thrasher, sage sparrow, and Brewer sparrow were found nesting in no other community. The greater amount of

cover of the greasewood community was utilized to a great extent by various animals to escape the high midday temperatures. Rabbit and bird counts tended to be higher during midday than they were in the morning and evening hours, and total bird populations increased as the summer progressed and the daily temperatures became higher.

Those animals which were nocturnal or which lived in burrows, such as kangaroo rats and the burrowing owl, were most abundant in the more open communities such as shadscale, winterfat and tetradymia. In such communities the scattered dominants were more important as sources of food than as cover. The feeding habits of the kangaroo rats suggest that the presence of shadscale may be a very important factor in their distribution and abundance. Only a very limited number of resident birds occurred in such communities. The principal species was the desert horned lark which nested on the ground and found adequate protection for its nest beneath the low, scattered dominant shrubs of the shadscale and winterfat communities. The desert black-throated sparrow, on the other hand, was largely restricted to the tetradymia community where there was a combination of taller shrubs interspersed among the shorter ones. It nested regularly only in that community and utilized the taller shrubs as singing perches and nesting sites.

The rodents are among the most ecologically important minor influents of the biome. They constitute the principal food supply of the predatory mammals, birds and reptiles; they influence the growth and distribution of certain dominant and subdominant plants; and their burrows are utilized by many reptiles and invertebrates as avenues of escape from their natural enemies and as a means of avoiding lethal temperatures during midsummer. Their interactions not only include the consumption and storage of leaves and seeds, but through their burrowing activities and underground deposition of stored plant materials and excrement, they alter the chemical and physical composition of the soil to the extent that very noticeable changes are produced in the growth and distribution of certain plants.

Morphological adaptations of the plants in response to the xeric climatic conditions to which they are subjected were very pronounced. The dominants are all perennials, are widely spaced, and have shallow fibrous root systems which are supplemented by a long taproot in some species. The conservation of water is accomplished through morphological adaptations such as reduced leaf surfaces, heavy cutinization of the epidermis, extreme pubescence of the leaf surfaces, and defoliation during the dry summer season.

Most of the animals are characterized by morphological and physiological adaptations or by adaptive types of behavior which enable them to tolerate or evade the high temperatures, low humidity and lack of drinking water. Prevention of water losses from the body surfaces is reduced to a minimum by the chitinous exoskeleton of the diurnal insects; by the

(Continued on Page 307)

## APPENDIX A

Distributional list of mammals, birds, and reptiles. The species listed for the shadscale community also occurred throughout the minor edaphic communities of the shadscale area in White Valley and adjacent areas.

	Shad- scale	Tetra- dymia	Grease- wood	Sage- brush		Shad- scale	Tetra- dymia	Grease- wood	Sage- brush
<b>MAMMALS</b>					Cooper Hawk				
Black-nosed Bat					<i>Accipiter cooperii</i> (Bonaparte)			X	X
<i>Myotis subulatus melanorhinus</i> (Merriam)	X	X	X		Western Red-tailed Hawk				
Pallid Big Brown Bat					<i>Buteo jamaicensis calurus</i> Cassin	X		X	X
<i>Eptesicus fuscus pallidus</i> Young			X	X	Swainson Hawk				
Desert Pallid Bat					<i>Buteo swainsoni</i> Bonaparte	X	X	X	X
<i>Antrozous pallidus pallidus</i> (LeConte)	X				Golden Eagle				
Mexican Free-tailed Bat					<i>Aquila chrysaetos canadensis</i> (Linnaeus)	X		X	X
<i>Tadarida mexicana</i> (Saussure)	X	X			Southern Bald Eagle				
Nevada Long-tailed Weasel					<i>Haliaeetus leucocephalus leucocephalus</i> (Linnaeus)	X			X
<i>Mustela frenata nevadensis</i> Hall	X		X		Marsh Hawk				
Great Basin Spotted Skunk					<i>Circus cyaneus audsoni</i> (Linnaeus)	X	X	X	X
<i>Spilogale gracilis saxatilis</i> Merriam	X	X			Prairie Falcon				
Badger					<i>Falco mexicanus</i> Schlegel	X	X	X	X
<i>Taxidea taxus</i> sp.	X	X	X	X	Eastern Sparrow Hawk				
Kit Fox					<i>Falco sparverius sparverius</i> Linnaeus	X	X	X	
<i>Vulpes macrotis</i> sp.	X				*Sora Rail				
Coyote					<i>Porzana carolina</i> (Linnaeus)			X	
<i>Canis latrans lestes</i> Merriam	X	X	X	X	*Killed				
Bobcat					<i>Charadrius vociferus vociferus</i> Linnaeus			X	
<i>Lynx rufus</i> sp.	X	X			*Western Sandpiper				
Piute Ground Squirrel					<i>Ereunetes mauri</i> Cabanis			X	
<i>Citellus townsendi mollis</i> (Kennicott)	X	X	X	X	Western Mourning Dove				
Antelope Ground Squirrel					<i>Zenaidura macroura marginella</i> (Woodhouse)	X	X	X	X
<i>Citellus leucurus leucurus</i> (Merriam)	X	X	X	X	Western Burrowing Owl				
Wasatch Chipmunk					<i>Speotyto cunicularia hypugaea</i> (Bonaparte)	X	X	X	
<i>Eutamias minimus conobrinus</i> (Allen)				X	Long-eared Owl				
Pocket Gopher					<i>Asio otus wilsonianus</i> (Lesson)				X
<i>Thomomys bottae centralis</i> Hall	X	X	X		Nighthawk				
Nevada Pocket Mouse					<i>Chordeiles minor</i> sp.	X		X	X
<i>Perognathus longimembris nevadensis</i> Merriam	X	X	X		Nuttall Poor-will				
Long-tailed Pocket Mouse					<i>Phalaenoptilus nuttallii nuttallii</i> (Audubon)	X	X		X
<i>Perognathus formosus formosus</i> Merriam		X			Western White-throated Swift				
Great Basin Pocket Mouse					<i>Aeronautes saxatilis saxatilis</i> (Woodhouse)	X	X		
<i>Perognathus parvus olivaceus</i> Merriam				X	Broad-tailed Hummingbird				
Kangaroo Rat					<i>Selasphorus platycercus platycercus</i> (Swainson)	X	X		X
<i>Dipodomys microps bonnetillei</i> Goldman	X	X	X	X	Rufous Hummingbird				
Kangaroo Rat					<i>Selasphorus rufus</i> (Gmelin)	X			
<i>Dipodomys ordii cleripes</i> Durrant and Hall	X	X	X	X	Arkansas Kingbird				
Kangaroo Mouse					<i>Tyrannus verticalis</i> Say	X	X	X	X
<i>Micridipodops megacephalus paululus</i> Hall and Durrant	X	X	X		Ash-throated Flycatcher				
Grasshopper Mouse					<i>Myiarchus cinerascens cinerascens</i> (Lawrence)	X	X		
<i>Onychomys leucogaster brevicaudus</i> Merriam	X	X	X		Say Phoebe				
Harvest Mouse					<i>Sayornis saya saya</i> Bonaparte	X	X		X
<i>Reithrodontomys megalotis megalotis</i> (Baird)			X	X	Great Salt Lake Horned Lark				
White-footed Mouse					<i>Otocoris alpestris utahensis</i> Behle	X	X	X	X
<i>Peromyscus maniculatus sonoriensis</i> (LeConte)	X	X	X	X	Violet-green Swallow				
White-footed Mouse					<i>Tachycineta thalassina lepida</i> Mearns	X	X		
<i>Peromyscus crinitus pergracilis</i> Goldman		X			*Barn Swallow				
Desert Pack Rat					<i>Hirundo rustica erythrogaster</i> Bodlaert			X	
<i>Neotoma lepida lepida</i> Thomas		X			American Magpie				
Black-tailed Desert Jack Rabbit					<i>Pica pica hudsonia</i> (Sabine)				X
<i>Lepus californicus deserticola</i> Mearns	X	X	X	X	American Raven				
Cottontail Rabbit					<i>Corvus corax sinuatus</i> Wagler	X	X	X	X
<i>Sylvilagus nuttallii grangeri</i> (Allen)	X	X		X	Pifion Jay				
Pronghorn Antelope					<i>Cyanoccephalus cyanoccephalus</i> (Wied)				X
<i>Antilocapra americana americana</i> (Ord)	X	X	X	X	Rock Wren				
<b>BIRDS</b>					<i>Salpinctes obsoletus obsoletus</i> (Say)		X		X
*SPECIES OBSERVED ONLY AT TULE SPRINGS IN THE GREASEWOOD COMMUNITY.					Western Mockingbird				
*Treganza Great Blue Heron					<i>Mimus polyglottus leucopterus</i> (Vigors)			X	X
<i>Ardea herodias treganzai</i> Court			X		Sage Thrasher				
*Common Mallard					<i>Oreoscoptes montanus</i> (Townsend)	X	X	X	X
<i>Anas platyrhynchos platyrhynchos</i> Linnaeus			X		Mountain Bluebird				
Western Turkey Vulture					<i>Sialia currucoides</i> (Bechstein)				X
<i>Calhates aura teler</i> Friedmann	X	X	X	X	Western Gnatcatcher				
Sharp-shinned Hawk					<i>Poliophtila caerulea amoenissima</i> Griener				X
<i>Accipiter striatus velox</i> (Wilson)	X		X		Great Basin Shrike				
					<i>Lanius ludovicianus nevadensis</i> Miller	X	X	X	X



	Shad-scale	Tetra-dymia	Grease-wood	Sage-brush		Shad-scale	Tetra-dymia	Grease-wood	Sage-brush
BIRDS					Northern Sage Sparrow				
*Yellow Warbler					<i>Amphispiza belli nevadensis</i> (Ridgway).....	X	X	X	X
<i>Dendroica aestiva</i> sp.....			X		Western Chipping Sparrow				
*Northern Audubon Warbler					<i>Spizella passerina arizonae</i> Coues.....	X	X		X
<i>Dendroica auduboni</i> sp.....			X		Brewer Sparrow				
*Western Yellow-throat					<i>Spizella breweri breweri</i> Cassin.....	X	X	X	X
<i>Geothlypis trichas occidentalis</i> Brewster.....			X		White-crowned Sparrow				
*Long-tailed Chat					<i>Zonotrichia leucophrys</i> sp.....	X	X	X	X
<i>Icteria virens auricollis</i> Bonaparte.....			X		Slate-colored Fox Sparrow				
English Sparrow					<i>Passerella iliaca schistacea</i> Baird.....				X
<i>Passer domesticus domesticus</i> (Linnaeus).....	X				*Song Sparrow				
Yellow-headed Blackbird					<i>Melospiza melodia</i> sp.....			X	
<i>Xanthocephalus xanthocephalus</i> (Bonaparte).....	X		X		REPTILES				
Red-winged Blackbird					Collared Lizard				
<i>Agelaius phoeniceus</i> sp.....	X		X		<i>Crotaphytus collaris baileyi</i> (Stejneger).....		X		
Brewer Blackbird					Leopard-lizard				
<i>Euphagus cyanocephalus cyanocephalus</i>					<i>Crotaphytus wislizenii</i> Baird & Girard.....	X	X	X	X
(Wagler).....	X	X	X	X	Brown-shouldered Uta				
Nevada Cowbird					<i>Uta stansburiana stansburiana</i> (Baird & Girard).....	X	X	X	X
<i>Molothrus ater artemisiae</i> Grinnell.....	X		X		Sagebrush Lizard				
House Finch					<i>Sceloporus graciosus graciosus</i> (Baird & Girard).....			X	X
<i>Carpodacus mexicanus</i> sp.....	X				Desert Horned-toad				
Pale Goldfinch					<i>Phrynosoma platyrhinos</i> Girard.....	X	X	X	X
<i>Spinus tristis pallidus</i> Mearns.....	X	X			Whip-tail Lizard				
Green-tailed Towhee					<i>Cnemidophorus tessellatus tessellatus</i> (Say).....	X	X	X	X
<i>Oberholseria chlorura</i> (Audubon).....			X	X	Striped Racer				
Lark Bunting					<i>Coluber taeniatus taeniatus</i> (Hallowell).....	X	X	X	X
<i>Calamospiza melanocorys</i> Stejneger.....	X		X		Gopher-snake				
*Nevada Savannah Sparrow					<i>Pituophis catenifer deserticola</i> Stejneger.....	X	X	X	X
<i>Passerculus sandwichensis nevadensis</i> Grinnell			X		Long-nosed Snake				
Western Vesper Sparrow					<i>Rhinoceros lecontei</i> Baird & Girard.....	X			
<i>Poocetes gramineus confinis</i> Baird.....	X	X	X	X	Rattlesnake				
Western Lark Sparrow					<i>Crotalus viridis lutosus</i> (Klauber).....	X	X	X	X
<i>Chondestes grammacus strigatus</i> Swainson.....	X	X		X					
Desert Black-throated Sparrow									
<i>Amphispiza bilineata deserticola</i> Ridgway.....	X	X	X	X					

## APPENDIX B

Distributional list of identified invertebrates collected in quantitative samples.

	Shad-scale	Tetra-dymia	Grease-wood	Sage-brush		Shad-scale	Tetra-dymia	Grease-wood	Sage-brush
ARANEIDA					ACARINA				
Argiopidae—					Caeculidae—				
<i>Araneus carbonarius</i> (C. Koch).....	X	X			<i>Caeculus nigripes</i> Bks.....	X	X		
<i>Araneus</i> sp.....	X		X		Erythraeidae—				
<i>Metespeira fazi</i> Gertsch & Ivie.....	X	X	X		<i>Atomus arvensis</i> Bks.....	X	X		X
<i>Metespeira</i> sp.....		X	X	X	<i>Atomus lepidonotus</i> Bks.....	X			
Dictynidae—					<i>Erythraeus</i> sp.....	X	X	X	
<i>Dictyna reticulata</i> Gertsch & Ivie.....			X	X	Tetranychidae—				
<i>Dictyna</i> sp.....	X	X	X		<i>Bryobia praetiosa</i> Koch.....		X	X	
Oxyopidae—					Trombidiidae—				
<i>Oxyopes rufipes</i> Banks.....		X	X	X	<i>Trombidium</i> sp.....			X	
Salticidae—					COLLEMBOLA				
<i>Dendryphantus</i> sp.....	X		X	X	<i>Deuteroaminturus</i> sp.....		X		
<i>Eucarcha hoyi</i> (Peckham).....	X		X		<i>Sminthurus</i> sp.....	X	X		
<i>Habrocestum</i> sp.....			X		ORTHOPTERA				
<i>Icius</i> sp.....				X	Acrididae—				
<i>Pellenes</i> sp.....	X	X	X	X	<i>Aeoloplus tenuipennis tenuipennis</i> Scudder ..	X	X	X	
<i>Phidippus formosus</i> Peckham.....			X		<i>Melanoplus complanatus canonicus</i> Scudder.....				X
<i>Phidippus</i> sp.....		X	X	X	<i>Melanoplus mexicanus mexicanus</i> (Saussure).....				X
<i>Sassacus papenhoei</i> Peckham.....			X		<i>Melanoplus</i> sp.....		X	X	X
<i>Titanebo</i> sp.....		X			<i>Trimerotropis gracilis gracilis</i> (Thomae).....				X
Theridiidae—					<i>Trimerotropis pallidipennis pallidipennis</i> (Burm.).....	X			X
<i>Eurypis scriptipes</i> Banks.....			X		<i>Xanthippus lateritius</i> Saussure.....	X	X		
Thomisidae—					THYSANOPTERA				
<i>Misumenops celer</i> (Hentz).....	X	X	X		<i>Anaphothrips</i> sp.....		X		
<i>Misumenops</i> sp.....	X	X	X		<i>Frankliniella occidentalis</i> Perg.....		X		
<i>Philodromus virescens</i> Thorell.....			X	X	<i>Thrips</i> sp.....			X	
<i>Philodromus</i> sp.....	X		X	X					
<i>Xysticus cunctator</i> Thorell.....			X	X					
<i>Xysticus</i> sp.....			X	X					

	Shad- scale	Tetra- dymia	Grease- wood	Sage- brush		Shad- scale	Tetra- dymia	Grease- wood	Sage- brush
HEMIPTERA					Coccidae—				
Anthracoridae—					<i>Orthezia</i> sp. (near <i>artemisiae</i> )	X		X	
<i>Orius tristicolor</i> (White)	X	X	X	X	Fulgoridae—				
Corixidae—					<i>Deserta bipunctata</i> Ball	X			X
<i>Corixus viridicatus</i> Uhler				X	<i>Hysteropterum cornutum</i> Mel.			X	X
Lygaeidae—					<i>Oecleus fulviflorus</i> Ball	X			
<i>Geocoris</i> sp.			X		<i>Oecleus nanus</i> Van D.		X		
<i>Nysius californicus</i> Stal.	X	X	X		<i>Oliarus</i> sp.			X	
<i>Nysius ericae</i> (Schilling)		X			<i>Orgerius minor</i> Ball	X			
Miridae—					<i>Scolopis uhleri marginatus</i> Ball	X		X	
<i>Adelphocorus superbus</i> Uhl.		X	X		Membracidae—				
<i>Chlamydatus uniformis</i> Uhl.				X	<i>Enchenopa permutata</i> Van D.			X	
<i>Europiella decolor</i> (Uhl.)				X	Psyllidae—				
<i>Europiella</i> sp.				X	<i>Aphalara</i> sp.				X
<i>Lopidea</i> (n. sp.)				X					
<i>Lygus elisus</i> Van D.		X		X	COLEOPTERA				
<i>Lygus</i> sp.		X			Anthicidae—				
<i>Megalopsallus rubropictus</i> Kent.			X		<i>Anthicus</i> sp.	X		X	X
<i>Megalopsallus</i> sp.		X	X		Chrysomelidae—				
<i>Parthenicus</i> sp.			X		<i>Chaelocnema</i> sp.				X
<i>Phylloidea</i> sp.	X				<i>Monozia</i> sp.	X	X	X	X
<i>Psallus pictipes</i> (Van D.)		X	X		<i>Pachybrachis</i> sp.	X	X	X	X
<i>Psallus</i> sp. (No. 1)	X	X	X		<i>Phyllotreta</i> sp.			X	X
<i>Psallus</i> sp. (No. 2)		X			Cleridae—				
<i>Rhinacloa forticornis</i> Reut.			X		<i>Hydnocera discoides</i> Lec.	X			
<i>Sthenarus humeralis</i> Van D.			X		<i>Hydnocera scabra</i> Lec.	X		X	X
<i>Strongylocoris</i> (n. sp.)	X	X		X	<i>Hydnocera</i> sp.		X		
<i>Tuponia</i> sp.				X	Coccinellidae—				
Nabidae—					<i>Ezochomus septentrionis</i> Wa.	X			
<i>Nabis alternatus</i> Parshley	X	X	X	X	<i>Hippodamia apicalis</i> Csy.				X
Pentatomidae—					<i>Hippodamia convergens</i> Guer.			X	
<i>Chlorochroa sayi</i> Uhl.			X		<i>Hippodamia</i> sp.				X
<i>Thyanata custator</i> (Fabr.)				X	<i>Hyperaspis fastidiosa</i> Csy.			X	
<i>Thyanata rugulosa</i> (Say)			X	X	<i>Hyperaspis fimbriolata</i> (Melsh.)				X
Pisumidae—					<i>Hyperaspis lateralis montanica</i> Csy.				X
<i>Pisuma depressa</i> McAtee			X		<i>Hyperaspis pleuralis aterrima</i> Csy.	X			
<i>Pisuma explanata</i> McAtee			X	X	<i>Hyperaspis tenebrata</i> Lec.				X
Reduviidae—					<i>Hyperaspis</i> sp.			X	
<i>Sinea</i> sp.			X	X	<i>Seymouria</i> sp.				X
<i>Zelus socius</i> Uhl.			X		Cureulionidae—				
HOMOPTERA					<i>Apion sordidum</i> Smith				X
Aphididae—					<i>Cercopea artemisiae</i> Pierce		X		X
<i>Aphis bonnevillensis</i> Knlt.			X		<i>Eupagoderes varius</i> Lec.	X	X		
<i>Epameibaphis frigida</i> (Oest.)	X				<i>Promecolatus densus</i> Csy.				X
Cercopidae—					Dermestidae—				
<i>Clastoptera brunnea</i> Ball				X	<i>Cryptorhopalum</i> sp.			X	
Chermidae—					Meloidae—				
<i>Paratrioxys cockerelli</i> (Sulc.)		X			<i>Epicaula maculata</i> (Say)				X
Cicadellidae—					Melyridae—				
<i>Aceratagallia cinerea</i> (O. & B.)	X	X			<i>Attalus</i> sp.	X		X	X
<i>Acinopterus</i> sp. (No. 1)			X		<i>Dasytastes ruficollis</i> (Ulke)	X	X		
<i>Acinopterus</i> sp. (No. 2)				X	<i>Listrus</i> sp.		X	X	X
<i>Athyanus frigidus</i> Ball				X	<i>Trichochrous</i> sp.		X	X	
<i>Ballana</i> sp.				X	Mordellidae—				
<i>Ceratagallia artemisia</i> Oman	X	X		X	<i>Mordellistena commata</i> Lec.			X	
<i>Ceratagallia dondia</i> (Oman)		X	X		<i>Mordellistena aspersa</i> Melsh.	X			
<i>Empoasca nigra typhlocyboidea</i> G. & B.				X	LEPIDOPTERA				
<i>Empoasca</i> sp. (nigra group)		X	X	X	Coleophoridae (Pupae)		X		X
<i>Empoasca</i> sp. (aspersa group)			X	X	Ethmiidae (Larvae)		X		
<i>Errhonus aridus</i> (Ball)	X	X		X	Gelechiidae (Larvae)	X		X	
<i>Eutettix insanus</i> Ball	X				Geometridae (Larvae)			X	X
<i>Eutettix tenellus</i> (Baker)	X		X		Olethreutidae (Larvae)		X	X	
<i>Exitianus obscurinervis</i> (Stal.)	X	X		X	Phalaenidae (Larvae)			X	
<i>Neosteles neglectus</i> (DeL. & D.)		X	X		Pterophoridae (Larvae)				X
<i>Norvellina clarivada</i> (Van D.)			X		Pyraustidae (Larvae)		X		
<i>Ophiola clavata</i> (Ball)			X	X	DIPTERA				
<i>Xerophloea viridis</i> (F.)			X	X	Agromyzidae—				
Cicadidae—					<i>Agromyza</i> sp. (sirens Lw. group)			X	
<i>Neoplatypedia constricta</i> Dan's				X	<i>Agromyza</i> sp.	X		X	
<i>Platypedia lutea</i> Dan's			X		<i>Leucopis</i> sp.	X		X	

	Shad- scale	Tetra- dymia	Grease- wood	Sage- brush
DIPTERA				
Anthomyiidae—				
<i>Hylemya</i> sp. ....		X	X	
Asilidae—				
<i>Cyrtopogon</i> sp. ....				X
Bombyliidae—				
<i>Geron</i> sp. (No. 1) .....	X	X	X	X
<i>Geron</i> sp. (No. 2) .....				X
<i>Mythcomyia</i> sp. ....				X
Ceratopogonidae—				
<i>Culicoides variipennis</i> (Coq.) .....			X	
Chironomidae—				
<i>Spaniotoma</i> sp. ....			X	
Chloropidae—				
<i>Madiza</i> sp. ....		X		
<i>Ocinella</i> sp. ....	X	X	X	
Culicidae—				
<i>Aedes</i> sp. ....			X	
Drosophilidae—				
<i>Scaptomyza graminum</i> Fallén .....			X	
Empididae—				
<i>Drapetis</i> sp. ....	X		X	
Ephydriidae—				
<i>Hydrellia</i> sp. ....		X	X	X
Otitidae—				
<i>Euzesta nitidiventris</i> Lw. ....	X	X	X	X
<i>Euzesta</i> (Probably new species) .....	X	X	X	
Rhagionidae—				
<i>Chrysopilus</i> sp. ....		X		
Sapromyzidae—				
<i>Caliope variceps</i> (Cog.) .....	X			
Sarcophagidae—				
<i>Eumacronychia</i> sp.? .....		X		
Scenopinidae—				
<i>Scenopinus</i> sp. (near <i>nubilipes</i> Say) .....	X		X	
<i>Scenopinus</i> sp. ....			X	
Tachinidae—				
<i>Plagia americana</i> Coq. ....			X	
<i>Zenilia</i> sp. ....			X	
Trypetidae—				
<i>Trypanea abstersa</i> Lw. ....			X	
<i>Trypanea</i> sp. ....		X		

	Shad- scale	Tetra- dymia	Grease- wood	Sage- brush
HYMENOPTERA				
Callimomidae—				
<i>Callitome</i> sp. ....		X		
Chalcididae—				
<i>Halticella</i> sp. ....		X		
Elachertidae—				
<i>Elachertus</i> sp. ....				X
Encyrtidae—				
<i>Anagrus</i> sp. ....	X		X	
<i>Chalcaspis phenacoci</i> Ashm. ....			X	X
<i>Copidosoma</i> sp. ....			X	
Eulophidae—				
<i>Euderus</i> sp. ....			X	
Eurytomidae—				
<i>Eurytoma</i> sp. ....			X	
<i>Rileya</i> sp. ....		X		
Halictidae—				
<i>Halictus (Chloralictus) sparsus</i> Robt. ....	X			
Microgasteridae—				
<i>Halictoptera</i> sp. ....			X	X
Pteromalidae—				X
Scelionidae—				
<i>Leptacis</i> sp. ....		X		
<i>Platygaster</i> sp. ....		X	X	X
Tetrastichidae—				
<i>Tetrastichus</i> sp. ....			X	
Formicidae—				
<i>Camponotus (Myrmentoma)</i> sp. ....			X	X
<i>Crematogaster (Acrocoelia)</i> sp. ....	X	X		
<i>Dorymyrmex pyramicus</i> (Roger) .....	X	X		
<i>Formica fusca</i> L. var. ....			X	
<i>Formica manni</i> Whlr. ....			X	
<i>Formica neogagates</i> Emery .....			X	
<i>Formica neogagates lasioides</i> var. <i>retula</i> Whlr. ....			X	
<i>Formica obtusopilosa</i> Emery .....			X	X
<i>Formica</i> sp. ....			X	X
<i>Iridomyrmex</i> sp. ....				X
<i>Leptothorax rugatulus</i> Emery .....			X	
<i>Leptothorax</i> (n. sp.) .....	X	X		
<i>Monomorium minimum</i> (Buckley) .....			X	X
<i>Myrmecocystus mexicanus navajo</i> Whlr. ....	X	X		
<i>Myrmecocystus</i> sp. ....	X	X		
<i>Tapinoma sessile</i> (Say) .....		X	X	

impervious integument of the reptiles; by the lack of sweat glands in birds; and the profuse secretion by oil glands in the kangaroo rats. Conservation of water is facilitated by the excretion of the waste materials from the kidneys in the form of uric acid in insects, reptiles, and birds, and by effective reabsorption of water in the renal papilla of kangaroo rats. The majority of the mammals are nocturnal, and remain within burrows during the day in a microclimate which is less conducive to water losses from their body surfaces. The diurnal animals become less active during the hotter hours of the day and even some of the nocturnal species such as the kangaroo rats and honey ants were found to delay their time of emergence from their burrows until later hours of the night as daily summer temperatures increased.

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SYMPOSIUM ON

**DYNAMICS OF PRODUCTION IN  
AQUATIC POPULATIONS**

AT A JOINT MEETING OF

THE AMERICAN SOCIETY OF ZOÖLOGISTS  
THE ECOLOGICAL SOCIETY OF AMERICA  
THE LIMNOLOGICAL SOCIETY OF AMERICA

ST. LOUIS, MISSOURI

MARCH 28, 1946

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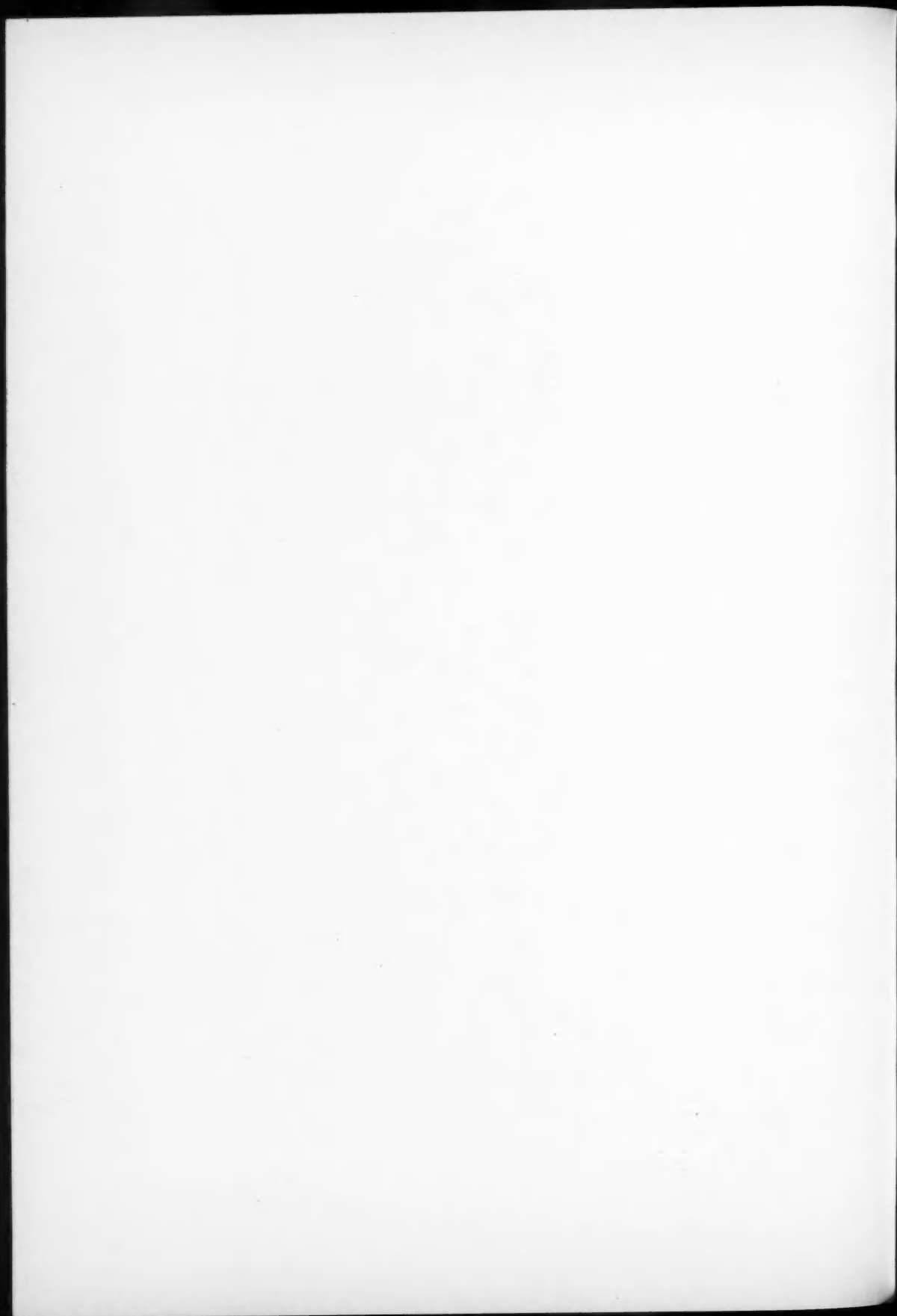
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SOME OBSERVATIONS ON THE HISTORY AND SCOPE  
OF POPULATION ECOLOGY

THOMAS PARK

*Hull Zoölogical Laboratory, The University of Chicago*



## SOME OBSERVATIONS ON THE HISTORY AND SCOPE OF POPULATION ECOLOGY<sup>1</sup>

As ecological research progresses and as ecological principles are formulated the study of ecology gradually but steadily emerges from a potpourri towards a coherent and more rigorous science. Population biology is contributing notably to this emergence—a point I wish to document briefly in this paper. During the last half of the Nineteenth Century ecology was just beginning to attain a self-conscious status. In 1869 Haeckel, undoubtedly influenced by Buffon's definition of bionomics and John Stuart Mill's and St. Hilaire's definitions of ethology, coined the word "oekologie" and defined it as "... comprising the relation of the animal to its organic as well as its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes in contact."

Although many published papers had a distinct ecologic content prior to this definition their major focus lay nevertheless in such peripheral fields as "natural history," "taxonomy," "adaptational morphology," and "physiology," the more strictly ecological aspects being subordinate. The definition of Haeckel, along with other pioneer publications that followed it during the next forty or so years, thus stimulated biologists to think about the total environmental relations of organisms in broader and more synthetic terms.

It is pertinent for the later development of this paper to mention the names of four individuals who furthered the growth of ecology not only by their own distinguished efforts but even more because they symbolize certain of the significant areas of study within which later Nineteenth Century ecology developed. The four are Semper, Möbius, Forbes, and Petersen.

C. Semper (1881) stressed the distinction between the physiology of organs and that of organisms considered as wholes in relation to their environment—a distinction fundamental for autecology.

K. Möbius, in his now-classical statement about an oyster bed considered as a "biocenose," presented a clear description of a relatively simple yet integrated community. He focussed attention on the ineluctable interdependence between the natural populations comprising the community instead of on particular habitat relations exhibited by species.

S. A. Forbes (1887) carried the concept of communities further and his essay "The lake as a microcosm," although brief, is such a mature document that many of the ideas of modern community analysis are foreshadowed there.

C. G. Joh. Petersen, perhaps most widely known for his contributions to the fishing industry, actually view fishery biology in a broad, ecological fashion. He insisted that fish populations are not isolated groups independent of their environment; he stressed the relation of growth-rate and food supply to production by populations of fishes, and he effectively applied quantitative methods to the study of ocean bottom fauna.

A detailed discussion of the historical status of ecology as of 1900 is not necessary here. For our present purpose it is sufficient to make these six points: (1) ecology had attained a certain intellectual coherence in that it was beginning to be recognized as an integral part of biological science; (2) significant research, largely of physiological character, was under way concerned with the growth, toleration, behavior, and survival of individual organisms as affected by specific factors of the external environment (autecology); (3) natural history studies had passed their height as such and, without losing either their significance or charm, were being assimilated by approaches of a more analytical nature; (4) with a background for community studies established by such writers as Möbius and Forbes among the zoologists, and Warming, Cowles, and Clements among the botanists this subject was poised awaiting the enthusiastic, perhaps even overenthusiastic, development that was to come during the next several decades; (5) ecology and evolution were drawing closer together through studies of natural selection and of isolation, and (6) the population approach to ecological problems was but slightly utilized and a theoretical formulation of population ecology was essentially nonexistent.

The subject matter of animal ecology falls naturally into three major levels of biological organization: the individual organism, the population, and the community. Within each of these levels further compartmentalization is possible and desirable. Thus the population is commonly considered both as intra- and inter-species systems, and populations ranging from the relatively simple to the intricate are readily identified within both categories. It is a reasonable generalization that mixed-species groups exhibit a breadth of phenomena that tend to be more complex and varied, both qualitatively and quantitatively, than do single species groups and that communities

<sup>1</sup> A shorter version of this paper was presented as an introduction to the Symposium, "Dynamics of production in aquatic populations," held at St. Louis on March 28, 1946. The paper has been expanded at the suggestion of several individuals to provide a general, and somewhat historical, statement about population ecology. I am greatly indebted to the following for reading and criticizing the manuscript and offering suggestions: L. C. Birch, Marian Burton Frank, G. L. Clarke, G. P. DuShane, W. T. Edmondson, A. E. Emerson, R. W. Pennak, and W. E. Ricker.

exceed both in these respects. This generalization, of course, has its exceptions.

With the advance of animal ecology during the Twentieth Century it soon became apparent that certain sorts of ecological problems did not lend themselves to investigation either through the approach of autecology or through that of community studies. Even though such problems utilize many of the basic data dealing with the environmental relations of individual organisms, and, even though they frequently furnish in themselves a new category of knowledge necessary for community analysis and thus possess a certain extrapolative significance in the understanding of communities, they must be studied directly in their own right. These problems on recognition and exploitation rapidly grew into the now-active field of population ecology to which this Symposium is a contribution.

Modern population ecology did not spring from a single origin but drew instead upon the techniques, data, principles, and emphases of several fields. Some of these relationships are indicated in the accompanying diagram in which the vertical axis is to be thought of in a general way as a chronology. It is obvious that the diagram is not a complete representation of the growth of this phase of ecology. It is merely designed to illustrate what seem to be certain of the more significant historical trends.

A line so drawn as to bisect the figure places human demography and biometry in one family and the more traditionally biological components in another. These two categories, comprising the early antecedents of the field, come together later when population ecology as such becomes better established.

It is to be noted that there are no specific entries in the diagram pertaining to "applied" or "economic" studies. It is not realistic to represent these by a single notation since so many different fields, of both statistical and biological character, are involved. The more significant developments within applied biology have originated in economic entomology (especially the work dealing with the biotic and climatic control of insect pests), in fishery biology, and in the more thoughtful aspects of game and wild-life management.

Both biometry and human demography have contributed substantially to population ecology. This is true, not only in that these subjects possess such an obvious technical usefulness that they form an essential part of the armamentarium of every investigator, but, also, in that they stimulated a few quantitatively minded biologists to attack selected problems in the laboratory suggested by the statistical behavior of human populations, using particularly the fruit fly, *Drosophila melanogaster*. This is best illustrated by the work of Raymond Pearl

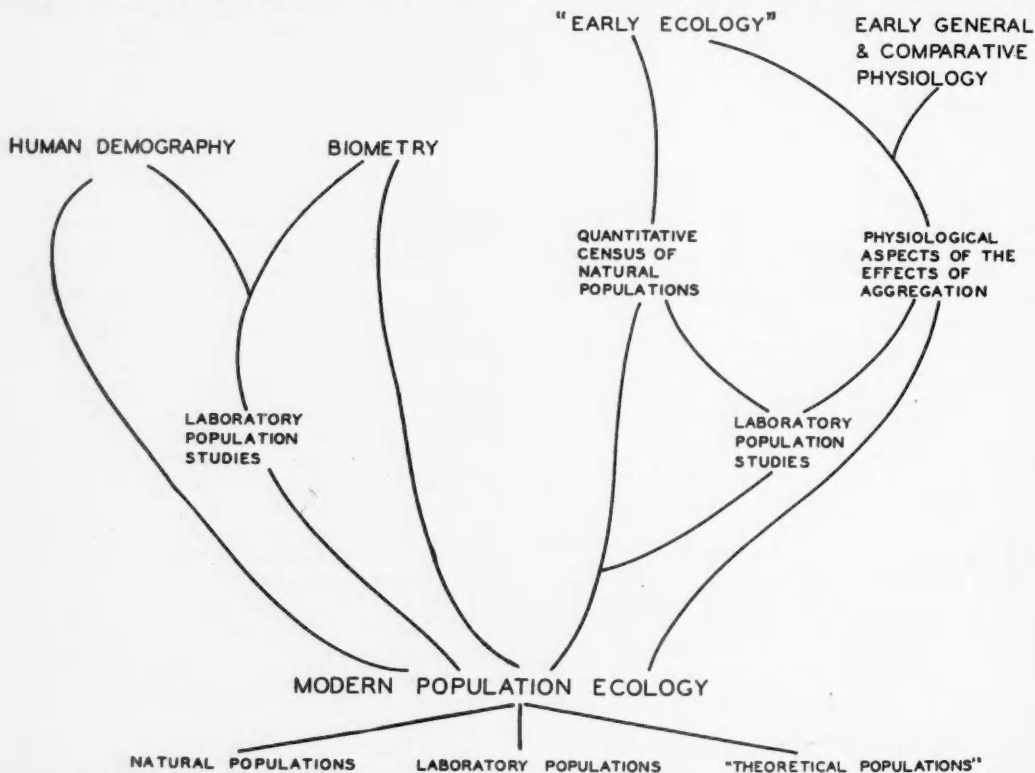


Fig. 1. Schematic representation of certain of the historical antecedents of population ecology.



and his colleagues who studied the form of population growth, who analyzed population density and demonstrated its significance in a relatively simple ecological system, and who investigated mortality (longevity) and natality in relation to certain ecological and genetic factors that influence them.

Something has already been said of the differentiation attained by animal ecology at the turn of the century and the entry "early ecology" in the diagram refers to the field as it then existed. During the early nineteen-hundreds plant and animal ecologists studied communities from rather diverse viewpoints. The conviction then arose that it is not sufficient to describe the interactions within a community exclusively in terms of taxonomic composition. The component species also must be considered as natural populations in which abundance is estimated both in space and time. Data such as these facilitate the drawing of conclusions, or at least of conjectures, that describe interspecies relationships in quantitative terms and then lead to the suggestion that the size or density of one population may be, and usually is, causally associated with that of another. The point can be simply illustrated by alluding to food-chains. Within a community it is essential to know what organisms as species constitute a food-chain nexus; e.g., green plants, key-industry herbivores, first and second order carnivores, parasites, incidental forms, etc. It is equally essential to know the numerical frequency of the species so that an evaluation can be made of the relation of these frequencies to each other and to the constancy and variability of the effective physical environment.

The felt need for such statistical information led to the development of census methods. It is in this way primarily that "early ecology" contributed to population studies both in a conceptual sense, namely, that quantitative knowledge about groups of organisms is required for community analysis, and in a methodological sense, namely, that means of accumulating this knowledge were devised. It is clear of course that biometry also played a rôle because the taking of a proper census requires an understanding of sampling in addition to sound statistical treatment of the counts once collected. The early interest in censusing feral populations did not arise wholly at the hands of academic ecologists. Applied biologists, who for purposes of pest control or conservation needed to know approximately how many forms occupied a defined area or volume, also entered this field.

Returning now to the diagram, we note that general and comparative physiology furnishes some thread for the fabric out of which population ecology is tailored. After Semper's pronouncement that the organism should be viewed as a responsive unit in its environment, there followed many studies on the relation of environmental factors ("conditions of existence") to organismic functions, especially those centering in growth and reproduction, behavior, and toleration.

In the second and third decades of this century a

few ecologists and physiologists were interested in the problem of animal aggregations. The significance of this phenomenon had been earlier appreciated by botanists, notably Clements, and certainly by a handful of philosophically minded biologists. But it was later that ecologists of physiological bent explored in the laboratory and field those effects induced by aggregation upon the aggregants and the habitat. W. C. Allee is an important figure in the synthesis of knowledge about this subject. In 1927 he discussed the methods of formation of aggregations; general factors conditioning aggregations, single and mixed species aggregations; integrative phenomena within aggregations, and the implications of aggregations for social organization.

Aggregation studies had a considerable effect upon the growth of population ecology. In the first place it follows that, since the investigation of aggregations is actually an aspect of population ecology in which the focus is directed towards particular problems and principles, a contribution in one field is likely to be a contribution in the other. Secondly, early aggregation research dealing as it did with the physiology of groups showed that such problems could be analyzed with some rigor—a technical advance of no small significance. Thirdly, these studies with their emphasis on crowding led to further consideration of population density from the viewpoint of general ecology but frequently studied experimentally using laboratory populations.

The trends indicated in the diagram suggest that study of populations in the laboratory was stimulated not only by human biology and by the increasing knowledge about animal aggregations but also by investigators whose main interest, originally at least, lay in the field. This is well illustrated by the research and background of R. N. Chapman. Chapman's earlier work was partly concerned with natural populations but he apparently became impressed by the complexity inherent in most field studies and sought means through which these problems could be attacked in the laboratory under carefully controlled, yet not too artificial, conditions. His search led him to the flour beetle, *Tribolium confusum*, which proved to be a fortunate choice for the experimental analysis of population phenomena. In a 1928 paper entitled "The quantitative analysis of environmental factors" Chapman developed his ideas of "biotic potential" and "environmental resistance" and, perhaps more importantly, illustrated by example how phenomena familiar in the field could be attacked experimentally. Despite the fact that Chapman's conclusions seem somewhat oversimplified his contribution is historically a significant one.

Even this rather cursory discussion of certain of the antecedents of population ecology makes it clear that many fields have contributed to its development. In its present dress the subject matter falls simply yet meaningfully into three practical categories: natural populations, laboratory populations, and "theoretical populations." No qualitative distinction is drawn, nor in my opinion should be, between

aquatic or terrestrial forms, between vertebrates or invertebrates, or in certain instances between animals and plants. Ideally, the population ecologist must be concerned with all sound data, imaginative hypotheses, and well-founded principles derived from study of populations irrespective of the taxonomy or habitats of the species considered. While he may prefer or be compelled to work with, say, fishes or plankton or insects or protista his background and interest should be such that he can recognize concepts common to all populations and therefore important for all of ecology as well as for much of biology.

Under this plan of operation workers in such seemingly diverse fields as oceanography, limnology, microbiology, entomology, ichthyology, herpetology, ornithology, mammalogy, and human biology thus produce not only basic knowledge about the group phenomena particular for the respective populations under study but also contribute towards that synthesis out of which a relatively comprehensive science of population ecology should emerge. When viewed in this light and when combined with the advances current in such active cognate fields as biostatistics and population genetics the future seems promising.

We have discussed the history of ecology by means of a diagram in which contributions stemming from various fields are indicated. This is a proper approach but the matter should not be left without mentioning that growth of the subject has probably been catalyzed all along the way by a feeling on the part of researchers that the phenomena of synecology (group ecology) should be expressed as quantitatively as possible. Community study to a large extent is still in a descriptive stage and, in my opinion at least, its further progression depends in part upon the progress of population ecology. On quite a few occasions, I suspect, ecologists have turned from research on communities to research on natural or laboratory populations simply because, as less complex systems, the latter promised more immediate reward in comprehending ecological phenomena. Nothing derogatory to community studies is implied in this statement. Probably the most important ultimate objective of ecology is an understanding of community structure and function from the viewpoint of its metabolism or energy relationships. (Lindeman 1942). A major reason for studying populations lies in the contribution that may be made towards this goal.

While it is not appropriate for the purpose of this Introduction to discuss in any detail the scope of modern population ecology, a few comments along this line do seem in order. These follow in part a short published summary (Thomas Park 1945).

There is no difficulty in understanding why the biologist studies cells or organisms. Population or group biology, however, is a younger field and as such its existence and significance is less well known. As mentioned earlier the population represents a level of organization "above" that of the organism. It follows from the fact that since it is composed

of many organisms a population possesses certain organismic features. In addition, however, it has a series of unique features that emerge because it is a unit reacting as a whole within its immediate environment. The latter phase is of especial significance.

The coordinating features of population ecology are, as already pointed out, (1) that the attributes of groups can be investigated and (2) that these attributes have many similarities even though the populations examined may seem quite diverse. There are real differences between populations, of course, and these afford valuable avenues of exploration. But it is primarily the similarities that provide population ecology with the common denominator from which biological generalizations can be derived.

The population biologist is concerned with the statistical consequences of reproduction (natality), of mortality, of dispersion, and with those environmental and hereditary conditions that affect them. Reproduction has the immediate effect of increasing the size of the group; mortality, of decreasing it, and dispersion can function in either direction depending upon the pattern it assumes. It is obvious that these factors operate not singly but in relation to each other. They should be thought of as compound factors in that their intensity at any moment of time depends upon a particular reticulum of antecedent, causal events. The interactions between natality, mortality, and dispersion confer upon populations a "growth-form" which, over an entire life-history, can be conveniently broken down into six periods: positive growth, equilibrium, oscillation, fluctuation, decline (negative growth), and extinction. Information about growth-form is fundamental for any population study. Growth-form is roughly analogous to knowledge of, say, the anthropometry of a man which provides a sort of general statement about his total, external structure, or to such physiological indices as basal metabolic rate, respiration rate, heart-beat frequency, and body temperature which evaluate in a way his total metabolic relationships.

A number of problems and phenomena are being studied by population ecologists using many species of organisms and diverse techniques. Probably the more important of these, excluding a group centering in evolution and speciation and best considered in conjunction with genetics, are as follows:

- (1) Studies, numerical in nature, describing the growth-form of populations.
- (2) The effect of various physical-chemical factors on population growth-form.
- (3) Analysis of population equilibrium.
- (4) The problems of underpopulation, optimal-population, and overpopulation.
- (5) The productivity of populations and factors that influence it.
- (6) The problem of the "optimal yield." (That is, to what extent can a population be exploited and still maintain itself?)
- (7) Description and analysis of population cycles.

- (8) Analysis of dispersion within and between populations.
- (9) Analysis of range and territory phenomena exhibited by natural populations.
- (10) Epidemiological aspects of the interactions between host and parasite populations.
- (11) Intra-species and inter-species competition.
- (12) The organization of social populations.
- (13) Improvements and extensions of population census techniques.
- (14) The integration of populations; how factors interact to control population phenomena.

Present day studies of natural or field populations are concerned largely with analysis of population growth-form and the various factors that influence it. Thus, censuses of groups are taken to determine, as first approximations at least, their size, density, and distribution. This may be followed by a survey of those conditions that appear to be correlated with the census findings. Meteorological factors in the case of terrestrial populations and physical and chemical qualities of the medium in the case of aquatic populations are often demonstrated, either singly or in combination, to affect a population's growth-form. The quality, quantity, and availability of food is another factor frequently studied. Biotic factors too are considered, notable among which are observations on host-parasite relationships from the viewpoint of two interacting populations, observations on predator-prey relations, and on a number of intra- and inter-species competitions for food, niches, mates and so on.

As discussed earlier, present day experimental or laboratory population studies proceed on the basis that, because it is usually difficult to assess population phenomena in nature, something is gained when relatively simple populations are studied in the laboratory under controlled conditions. An objection to this approach is that it may be artificial and therefore lack application for natural populations. A virtue is that the experimental approach facilitates an analysis that usually has a precision and interpretative significance not ordinarily possible in field work. The answer is, of course, that the two types of investigation complement each other and tend to draw together rather than apart. Also, by intelligent choice of species, project, and experimental conditions, it is usually possible to deal with problems in the laboratory that actually are not very artificial at all. The last point is well-illustrated in a recent paper by Elton (1946).

In the laboratory these forms have been the most studied: yeasts, free-living protozoa, rotifers, insects (especially granary beetles and members of other grain-inhabiting orders, fruit flies, chalcid flies, and certain of the social isoptera and hymenoptera), and, among the vertebrates, a few aquarium fishes, chickens, wrens, rodents, monkeys, and apes. The problems most studied thus far have been, for single species populations, population growth-form, and the relation of population density to reproduction and mortality; and for mixed-species popula-

tions, competition between two species for a common niche or for food, and host-parasite and predator-prey interactions. Unfortunately, there are few comprehensive investigations of dispersion, from the point of view of population ecology, for either natural or laboratory groups.

As indicated in the diagram there is also an approach that might be called, for want of a better designation, the study of theoretical populations. This is a conjectural field and it is yet too soon to evaluate its contributions to date or its future promise. It has been developed by such workers as Volterra and Lotka among the mathematicians and Bailey, Nicholson, Thompson, Kostitzin, and Jackson among those whose interests are more purely biological. In simplest terms this approach is concerned with the setting up of basic (but usually highly oversimplified) postulates about group interactions; reasoning, in mathematical form, as to what happens when the postulates operate in a particular situation, and, finally, testing the theoretical system by actual studies. Whatever the merits of this attack it is fair to conclude at this time that it has not been nearly as productive for population ecology as the statistical-probability attack has been for population genetics.

Some indication of the growing interest in population ecology is afforded by the fact that within the last decade three symposia, national in scope, have been directed to this field. The first, at Atlantic City in 1936, dealt with population phenomena exhibited by protozoa, cladocera, insects, and man. The second, at Richmond in 1938, dealt exclusively with insect populations considered from several points of view. The third, at Philadelphia in 1940, was limited to a reasonably detailed synthesis of experimental studies of protozoan populations.

In addition to these three programs, all of which have been published, I am aware of fifteen other public presentations given in this country between the years 1930 and 1942 that contain material with distinct implications for population ecology. To this group another symposium is added in the four papers following and is entitled "DYNAMICS OF PRODUCTION IN AQUATIC POPULATIONS."

This Symposium is obviously similar to its predecessors in its concern with selected phenomena of group biology. It is somewhat different in focus, however, in that it is primarily organized about a fundamental problem instead of about taxonomic categories. I believe it is noteworthy also that the Symposium attains a certain coherence because the participants, as ecologists convinced of the validity and fruitfulness of the population approach to ecological problems, have prepared their papers with this conviction in mind.

A word on the history of this Symposium is appropriate. After the participants had accepted their assignments, and after certain practical matters were settled, a brisk discussion by correspondence followed about selection of the topic. It was agreed that this should be broad enough to possess general ecological

significance beyond the confines of aquatic biology yet restricted enough so that specifically useful information could be assembled. The number of possible topics was reduced to six with each person expressing his first and second preferences. Through this procedure "DYNAMICS OF PRODUCTION" won by a wide margin.

This choice reflects both the interest and competence of the speakers as well as their belief that an understanding of production by populations is highly desirable because of its wide biological and economic implications.

The Symposium is so planned that the first two papers are general, the last two more specific, and all four are related to each other. Thus Doctor Clarke spends approximately half of his allotted time on questions of definition and concepts common to the entire Symposium. He then goes on to apply these ideas to a particular series of marine populations in the region of Cape Cod. This is followed by Doctor Pennak's paper in which productivity of fresh-water plankton populations is discussed. Doctor Edmondson then selects populations of a particular group of animals, the rotifers, and presents a more detailed treatment of production as it is understood for this phylum. Doctor Ricker concludes with vertebrate populations as illustrated by fishes and deals with concepts of production among these more highly integrated groups.

In closing this Introduction I should like to say that it is the hope of all members of the Symposium that the published product will not only be useful as a partial summary of knowledge about a significant problem but that, in revealing gaps in our information and suggesting new problems for investigation, it will stimulate additional research in population ecology.

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# DYNAMICS OF PRODUCTION IN A MARINE AREA

GEORGE L. CLARKE

*Biological Laboratories, Harvard University, and  
Woods Hole Oceanographic Institution*

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# DYNAMICS OF PRODUCTION IN A MARINE AREA

## INTRODUCTION

During recent years increasing attention has been given to the factors which underlie the productivity of natural areas and special interest has begun to center on the quantitative aspects of the relations involved. When a more exact and critical approach to the dynamics of production is attempted, it becomes obvious that ecologists, both practical and theoretical, have considered productivity from so many entirely different points of view that confusion, both in the concepts and in the terminology, has resulted. Before considering the productivity of any particular area, a general delineation of the specific concepts involved is highly desirable, and an agreement on terms is necessary. The attempt to clarify the subject which follows was prepared after a lively and penetrating consideration of the matter by the participants in this symposium.

## CONCEPTS OF PRODUCTION

All the ideas and measurements of productivity which have an ecological application, may be grouped under the following three fundamental concepts (Fig. 1):

*Standing crop*—the amount of organisms existing in the area at the time of observation.

*Material removed*—the amount of organisms removed from the area per unit time by man, or in other ways.

*Production rate*—the amount of organisms formed within the area per unit time.

All three of these major concepts of productivity are important, and are essential for a complete understanding of the operation of the area as an ecological complex. In addition, the quantities involved are to a certain extent mutually dependent.

## CONCEPTS OF PRODUCTIVITY

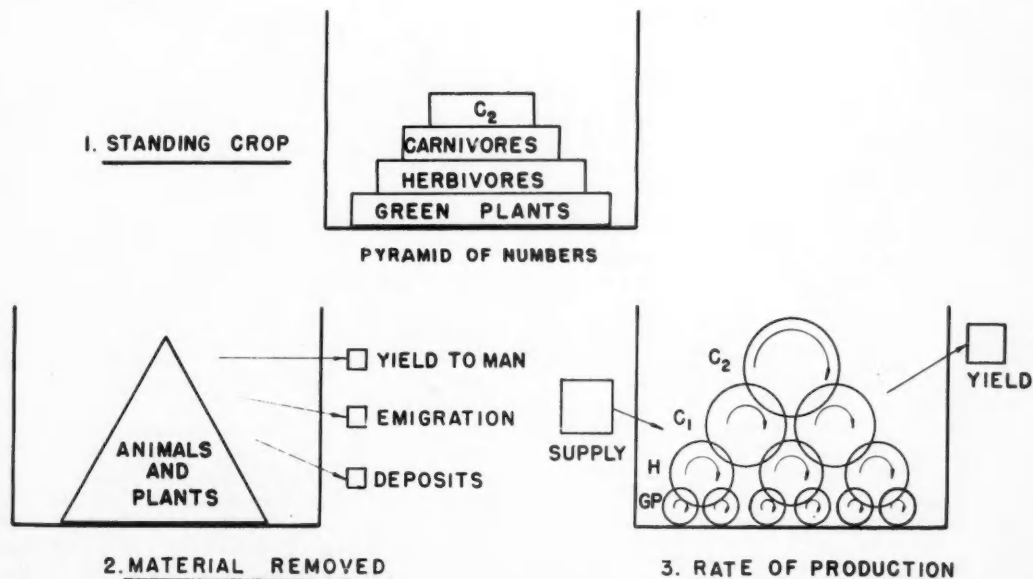


FIG. 1. Schematic representation of the three fundamental concepts of productivity: 1. *Standing Crop*—The number and kinds of organisms present in the area. Since abundance usually diminishes at the higher trophic levels, a pyramid of numbers is typical, extending in this case to secondary carnivores ( $C_2$ ). 2. *Material Removed*—The organisms, or their parts, which are permanently removed from the area by man or in other ways. 3. *Rate of Production*—The rates at which organisms are formed within the area. The interdependencies of the green plants (GP), herbivores (H), and primary and secondary carnivores ( $C_1$  and  $C_2$ ) are indicated.

To avoid ambiguity in discussing the ecological relationships of the area, it is suggested that the terms "productivity" and "production" be not used in referring to the standing crop or to the material removed unless a phrase is added to make the meaning clear (Ivlev 1945). Measurements made under any of the three categories may be stated in terms of number of individuals, weight or "biomass," energy content, or any other characteristic (such as chlorophyll content) which may be adequate for the given situation. Evaluation on the basis of energy content has the advantage that the efficiency of the utilization of the incident solar radiation may be calculated directly.

#### STANDING CROP

Measurements of the standing crop, and hence of the concentration, of the various species inhabiting the area are essential in judging the harmful or beneficial effect of crowding within the species, and the effectiveness with which dependent species can feed upon forage species. When applied to the exploitation of a natural population by man, the magnitude of the standing crop similarly influences the size of the catch per unit effort. However, a knowledge of the standing crop does not give any information as to the time which has been required to produce the crop, or its replaceability.

To illustrate these points, the changes of population size with time for three hypothetical situations are represented diagrammatically in Figure 2. In the first situation the growth rate of the population is much more rapid than in the second, but conditions are such that the same size of standing crop is attained provided that the season is sufficiently long for the maximum value to be reached. In this case, the final size of the standing crop gives no information as to the rate of net increase. If, however, the standing crop is measured before the asymptotic level is approached, the situation with the more rapid increase will have the larger stand-

ing crop. The size of the standing crop at any time is the result of the summation of the excess of production over destruction from the beginning of the growth of the population to the moment of observation.

In the third hypothetical situation, the same length of time is required for the population to reach a maximum size as in the second situation, but the maximum level reached is lower. In both situations, the population may fluctuate above and below the average limiting value (broken lines at right of curves), and since equilibrium is being maintained, at least temporarily, the average rate of production must be exactly balanced by the average rate of destruction. If the population is measured by number of individuals, the birth rate will exactly equal the death rate, regardless of the length of life of the individuals (Pratt 1943). It is possible that in some cases the rates of production and destruction may be higher in the area with the smaller average standing crop. Therefore, the magnitude of the standing crop cannot be taken as a measure of the rate of production, just as the level of water in a tank gives no clue as to the rates of inflow and outflow.

Since we have seen that the actual size of the standing crop after equilibrium has been reached is not determined by the rate of net increase nor by the rate of production, it is clear that the factor, or factors, which limit the final size of the population must be external influences, such as the accumulation of metabolites, or the lack of food (Pratt, 1943). Although a large population can thus exist without its own rate of production being high, it may require a large amount of food for its maintenance. Therefore, the existence of a large standing crop at one trophic level does imply the existence of either a large initial crop of the organism or nutrient, on which it feeds, or of a high rate of production, or supply, of this material.

#### MATERIAL REMOVED

The material removed from an area may fall into several categories. In the first place, the amount of organisms harvested by man during a certain period may be measured and designated as the *yield*. In addition, other organisms may be permanently removed from the area by wind or currents, or by emigration accomplished by the organisms' own locomotion.<sup>1</sup> Organisms which grow in the area but which are consumed, or die in other ways, and decompose so as to enter the ecological cycle again within the same area are not considered to be a yield in the sense recommended here. However, dead organic matter which has become permanently inaccessible, as for example, if buried under bottom deposits, is an irrevocable loss to the system, and hence forms another subdivision of the material removed.

These different subdivisions have in common the fact that in each instance the particular material

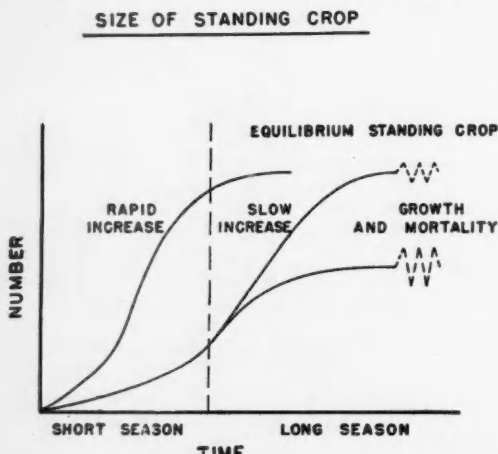


FIG. 2. Changes of population size with time in three hypothetical situations (for full explanation see text).

<sup>1</sup> This category may be also taken to include those organisms which are carried off by predators, other than man, provided that these predators do not form a functional part of the particular ecological unit being considered. Whether or not this limitation exists in any actual case may be difficult to decide.



which is removed from the area does not return again to that area. The amounts of the yield to man and of the other subdivisions may be added together to form a total amount of material removed from the system for the period considered. It is obvious that neither the total material removed nor the yield to man can be maintained if it is greater than the supply of new material entering the area during the same interval, either in the form of nutrient substances or of immigrants. Because of the inevitable loss of materials (and energy) at each level in the food chain, the yield will ordinarily be much smaller than the supply. Measurement of the ratio of yield to supply, and hence the efficiency of the formation of the yield, is therefore of great importance to the ecologist, to the conservationist, and to the farmer or fisherman, in order to ascertain whether the actual yield represents a needlessly low utilization or an over-exploitation of the area.

The yield may, in some cases, be improved by increasing the supply of materials to the area, as for example through the use of fertilizers, but even without artificial enrichment the yield of a particular species may sometimes be increased by adjusting its numbers to the optimum level and by curtailing the amount of material removed from the area in other ways. The *maximum potential yield* is the largest maintained amount of a species which may be removed from the area per unit time under the best population and environmental conditions which could be maintained.

A knowledge of the standing crop and of the material removed will not provide an understanding of the fundamental dynamic equilibria within the community upon which the productivity of the area ultimately depends. For an adequate grasp of the factors controlling abundance and yield, it is necessary to ascertain also the rates of formation of the interdependent types of plants and animals in the area.

#### PRODUCTION RATE

The concept of the production rate as the amount of organisms formed per unit time (per unit area or volume) is complicated by the fact that in most natural areas organic matter is being formed or transformed at several trophic levels simultaneously, i.e., by the plants and animals of the food chain which depend upon one another. In order for measurements of production rate to be useful it is necessary to keep separate the values for the various trophic levels and in each case to distinguish between gross and net rates of formation (Lindeman 1942).

These trophic relations among the components of the production pyramid may be represented diagrammatically, first, for a situation in which the constructive and destructive processes are equal so that there is no gain or loss in the amounts of organisms present at the end of the period over that at the beginning (Fig. 3). The amounts of energy contained in the organisms in the area at the beginning of the period, i.e., the standing crop, are indicated by the

rectangles at the left of the diagram. The rectangles at the right represent the amounts of energy absorbed at each trophic level and show *qualitatively* the transformations which the various portions undergo during the period. For simplicity only three trophic levels are indicated. Similar transformations could be added for secondary and tertiary carnivores, for parasites, and for saprophytes.

In tracing the energy and material through the production pyramid we may start with the incident light which falls upon the area. A portion of this light (small, in the aquatic environment) reaches the plant cells and is absorbed by them. A small portion of the absorbed energy appears as the carbohydrate which has been formed by photosynthesis ( $P_1$ ). The amount of material produced by this anabolic process (or of the energy represented) is termed the *gross plant production*. It has also been called the *primary production* because the animal substances which result from consuming the plants, and each other, are transformations of the original plant material, and thus represent alternative forms of the same material (and energy). In this sense the gross plant production may be considered a measure of the "total production" of the area, but because of the obvious ambiguity the latter term should be avoided. A large part of the gross production is lost as the result of catabolic processes. This loss may be measured by the amount of respiration. The remaining fraction of the gross production accounts for the new plant growth ( $P_2$ ) and this is termed the *net plant production*, or simply, the *plant production*, for unit area and time (cf. Riley, 1941a).

Since in the case considered there is no permanent increase or decrease in plant material, all of this new plant growth is destroyed and the energy transformed before the end of the period. Part of the plant material produced is consumed by herbivores and the remainder dies in some other manner and decomposes. In many situations a large proportion of the plant material consumed is not assimilated by the herbivores, but is passed through the gut undigested. This fraction ( $U$ ) may be added to that which has decomposed following destruction in other ways.

A similar analysis may be made of the material which enters into each of the successive trophic levels represented by the animals and colorless plants. At the herbivore level we start with the amount (or energy) of the food assimilated ( $P_1$ ), but much of this is lost in catabolic processes and the material which appears as the actual growth of the herbivore population ( $P_2$ ) is termed the *herbivore production*. It is assumed in this case that the herbivores are entirely destroyed during the period either by the carnivores or by death and decomposition from other causes. The same processes occur at the carnivore level with a resulting *carnivore production* for the period. The loss of the carnivore material at the top of the pyramid will of course all be accounted for by decomposition since none is consumed by predators.

## TROPIC RELATIONS IN THE PRODUCTION PYRAMID

## CASE I - NO GAIN OR LOSS FOR AREA

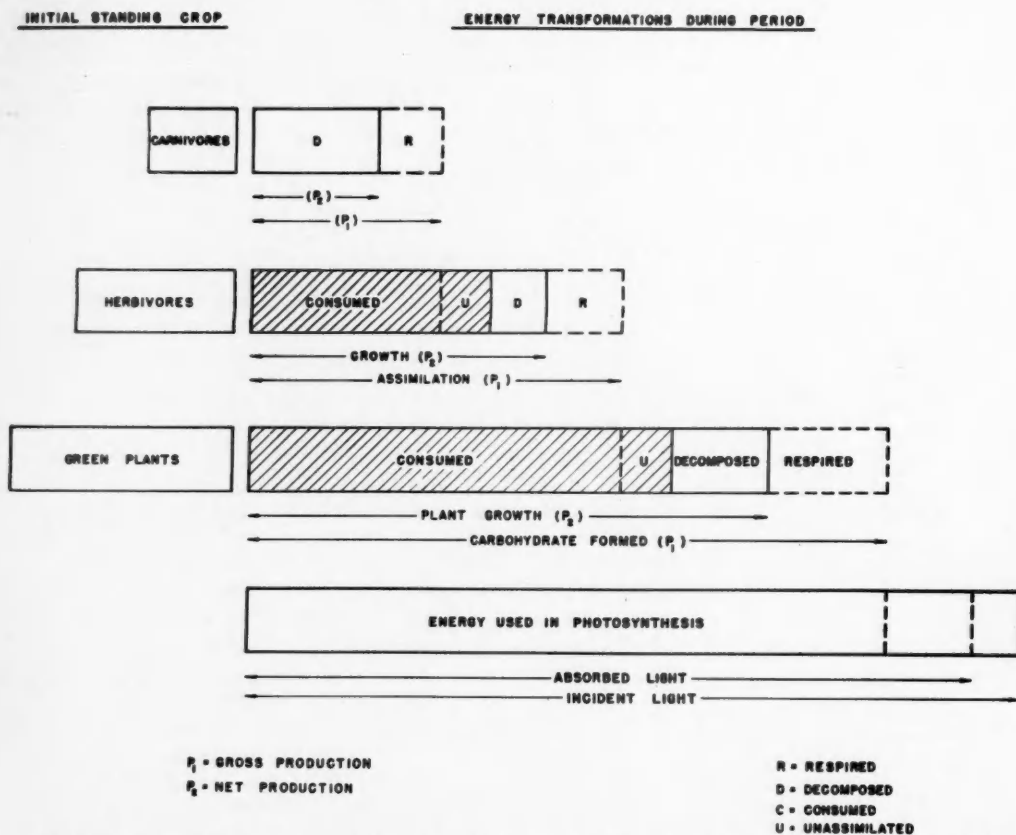


FIG. 3. Trophic relations in the production pyramid—Case 1: Relations shown qualitatively for a situation in which there is no net increase or decrease (see text).

At the end of the period for this hypothetical case of complete equilibrium the standing crop is of exactly the same magnitude as at the beginning and there has obviously been no yield. Production has been going on, however, at definite rates at the various levels, and in this case destruction of the materials has exactly balanced their formation during the period. The wheels of the factory have been turning but the products of the machinery have been taken in again as raw materials. Nevertheless for a critical understanding of the area it is essential for the ecologist to know what wheels are turning and at what rates. The magnitude of the standing crop at any moment does not give a measure of the rate at which production is going on since it is determined by the difference between the rates of production and destruction over the whole previous history of the population up to the time considered.

Let us consider now a second case, in which smaller

amounts of organisms are destroyed than are formed during the period (Fig. 4). Under these circumstances the growth ( $P_2$ ) of any one of the categories of organisms would be accounted for at the end of the period in three ways: one portion consumed, one portion decomposed, and one portion remaining in existence and representing an increment which may be termed the *net increase* ( $P_3$ ). The standing crop at the end of the period is consequently larger than at the beginning of the period by the amount of the net increase. In a situation in which the amount of destruction during the period was greater than the amount of production, the net increase ( $P_3$ ) would be negative, and the standing crop would be reduced.

If this surplus material is permanently removed from the system by man, it will constitute a yield. Obviously these organisms could not continue to be removed from the system in succeeding periods unless

## TROPIC RELATIONS IN THE PRODUCTION PYRAMID

## CASE 2 - NET INCREASE FOR AREA

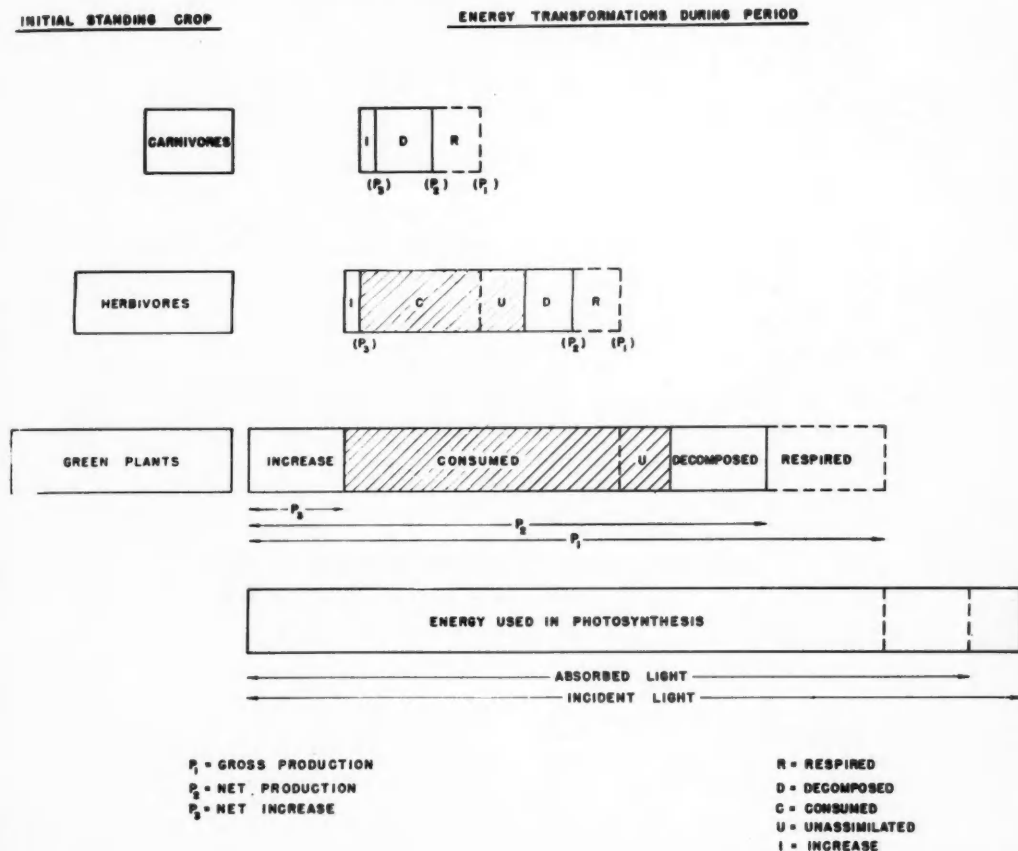


FIG. 4. Trophic relations in the production pyramid—Case 2: Relations shown qualitatively for a situation in which there is a net increase (see text).

an equal amount of material, as nutrients or in some other form, were added each period. If the organisms representing the net increase are not removed from the system, and if circumstances are such that they can continue in existence in the area, there will be a permanent increase in the size of the standing crop. Again, this can take place only to the extent to which an equivalent supply of nutrients or other materials are added to the area. The standing crops of lakes are frequently seen to increase in this way with the result that the lakes become more eutrophic and the process is known as *eutrophication*.

In the discussion of production rate thus far nothing has been said about the length of the period considered. The time required for each type of organism to complete its growth, to die and decompose, and to start the cycle over again is known as

its period of *turnover*. The length of the turnover period usually differs widely for the organisms at the different trophic levels of the production pyramid, and may differ for the same level in different situations and at different seasons of the year. The green plants of a terrestrial area may have essentially only one turnover per year, whereas the phytoplankton of an aquatic area may turnover within short periods varying widely from a few days to several weeks. In the latter case the same material may be used over again several times during the year, and it would thus have little meaning to add up the increments of growth for the whole year in an attempt to reach a "total" annual value. If the growth of the plants is measured as energy, it is permissible to summate the amount of energy which has been transformed during the year since the energy can be used

by the plants only once. A comparison may thus be made between the annual incident radiation and the energy content of the plants produced.

In the case of the organisms at successively higher trophic levels, both the materials and the energy are used over again one or more times. A summation of amounts of production at all trophic levels for a long period, such as a year, therefore similarly has little meaning. (Thienemann 1931).

The procuring of significant measurements of production rate is further complicated by the fact that growth, consumption, and decomposition may all be going on simultaneously under certain circumstances, as is frequently seen in aquatic situations. This difficulty may be dealt with by reducing the period considered to such a small size that instantaneous rates of growth, decomposition, etc., are obtained, or in other words by obtaining the differentials of the curves describing these processes. Production is therefore best measured as a set of rates applying to the gross production, net production, and net increase for each category of organisms or each trophic level. The term "productivity" has sometimes been used specifically for the rate at which assimilation (gross productivity) or growth (net productivity) is taking place since it is a measure of the rate at which the wheels of the system are turning. In view of the fact that this term is used in various broader senses to describe the capacity of an area to produce, it is preferable to employ the more explicit term, "production rate," and to specify the units of time and area considered. A mathematical development of these considerations is presented in the Appendix.

In cases in which the magnitudes of the rates of production at the different trophic levels can be measured, calculations may be made of the quantitative relationships of the various steps in the production. The following ratios, or efficiencies, are of interest (symbols refer to Fig. 4):

*For the plant:*

$$\begin{aligned}\text{Absorption} &= \frac{\text{absorbed light}}{\text{incident light}} \\ \text{Assimilation} &= \frac{\text{carbohydrates formed}}{\text{absorbed light}} \\ \text{Growth} &= \frac{\text{plant growth } (P_2)}{\text{carbohydrates formed } (P_1)} \\ \text{Increase} &= \frac{\text{net increase of plants } (P_2)}{\text{plant growth } (P_1)}\end{aligned}$$

*For the herbivore:*

$$\begin{aligned}\text{Consumption} &= \frac{\text{plants consumed (C including U)}}{\text{plant growth } (P_2)} \\ \text{Assimilation} &= \frac{\text{plants assimilated (C excluding U)}}{\text{plants consumed (C including U)}} \\ \text{Growth} &= \frac{\text{herbivore growth } (P_2)}{\text{herbivore assimilation } (P_1)} \\ \text{Increase} &= \frac{\text{net increase for herbivore } (P_2)}{\text{herbivore growth } (P_2)}\end{aligned}$$

*For the carnivore:*

$$\begin{aligned}\text{Consumption} &= \frac{\text{herbivores consumed (C including U)}}{\text{herbivore growth } (P_2)} \\ \text{Assimilation} &= \frac{\text{herbivores assimilated (C excluding U)}}{\text{herbivores consumed (C including U)}} \\ \text{Growth} &= \frac{\text{carnivore growth } (P_2)}{\text{carnivore assimilation } (P_1)} \\ \text{Increase} &= \frac{\text{net increase for carnivore } (P_2)}{\text{carnivore growth } (P_2)}\end{aligned}$$

The efficiencies given above are for the rates of the several processes at each of the trophic levels. Overall efficiencies may also be calculated, such as the ratio of the growth rate at one level to the growth rate at a previous level. Efficiencies for the growth or the net increase at any level based on the ratios of the energy content of the products to the incident radiation may also be found. On occasion it may be desirable to determine the ratios of assimilation, growth, net increase, etc., to the size of the existing standing crop. Similarly, the ratio of the rate at which the animals consume their food to the abundance of the food may be found instead of the ratio to the growth of the food.

The foregoing analysis of the processes involved in production no doubt will appear as an oversimplification. The material is intended, however, merely as a framework to assist in clarifying the fundamental relationships in a natural area and in placing them more readily on a quantitative basis. Illustrations of the use of these concepts of the dynamics of production will be found in the following section of the present paper and in the succeeding papers of this symposium (Pennak 1946, Edmondson 1946, and Ricker 1946).

#### PRODUCTION ON GEORGES BANK

The application of the foregoing concepts of productivity to a marine situation may now be illustrated for Georges Bank, an important fishing area off Cape Cod (Fig. 5). The size and relative inaccessibility of an offshore area of this sort render difficult the procuring of adequate information. As a result only a preliminary idea of the quantitative relationships can as yet be formed for Georges Bank although a very considerable number of biological and physical observations have been made. My present purpose is to point out the nature of the fundamental factors in a situation such as Georges Bank, and to consider the influence of special environmental conditions, such as the movement of water, in controlling the dynamics of production.

The chief components and interdependencies of Georges Bank are represented diagrammatically in Fig. 6. The green plants at the base of the production pyramid are the phytoplankton, and of these the diatoms are the most important. The herbivores, which constitute the next trophic level, are composed chiefly of planktonic crustacea. The copepods are generally the most prominent of the diatom-eating crustacea, but certain types of the larger



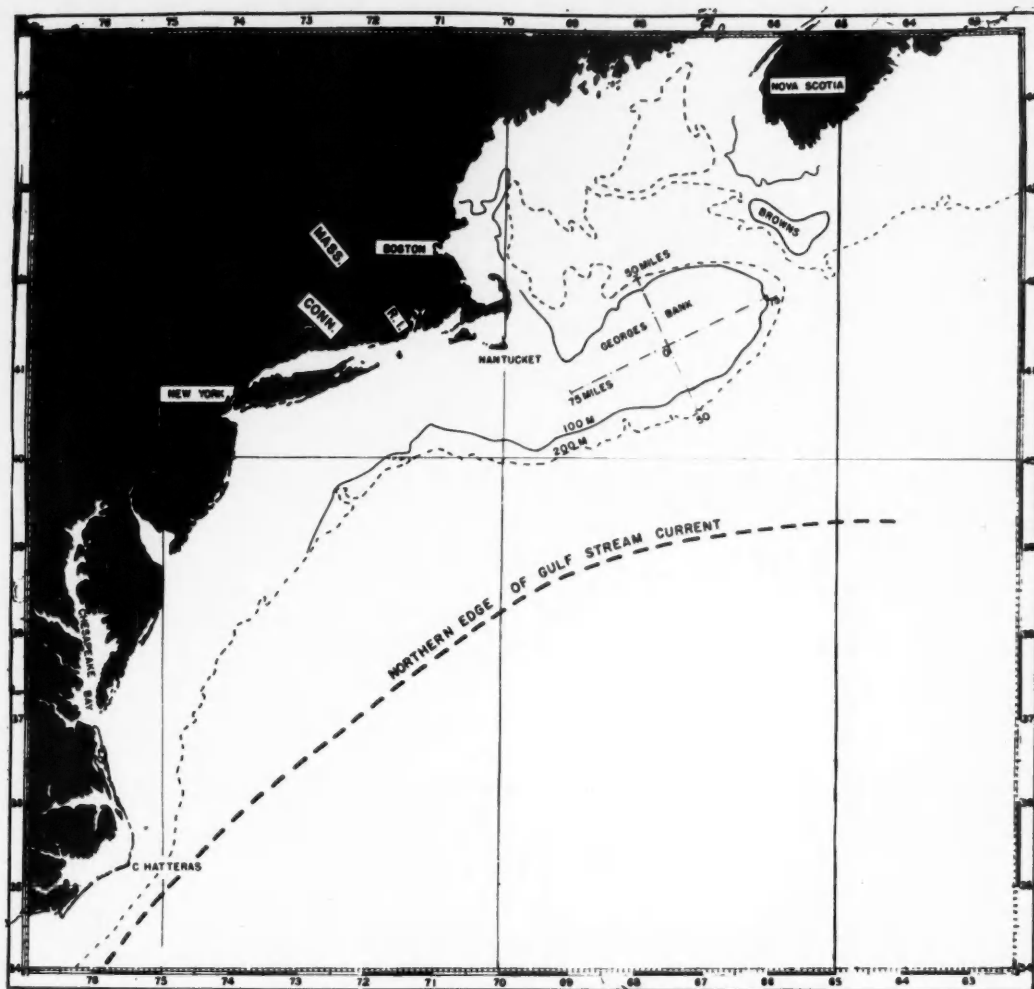


FIG. 5.—Location and dimensions of Georges Bank.

crustacea may also feed directly on the diatoms. The benthos obtains its food either directly from the phytoplankton, or indirectly by way of the detritus. Some bottom forms and some of the larger plankton forms, such as *Sagitta*, may feed extensively on the copepods and thus constitute a third trophic level. The various species of fish on Georges Bank, which depend upon the zooplankton, the benthos, or upon each other, form one or more additional trophic levels among the carnivores.

Let us consider first the circumstances in a marine area which affect the utilization of solar energy for the photosynthesis of the diatoms. The energy available is determined by the amount of solar radiation incident upon the sea surface minus that portion which is lost by reflection and by the absorption of the light by water and by particles other than the plant cells. In the region of Georges Bank the aver-

age energy per unit area reaching the sea surface for each month is shown in Table 1. These values are the monthly averages of the illumination which fluctuates each day from zero to the maximum reached at noon. The reduction in incident light with depth, due to absorption by the water and by dissolved and suspended material, has been measured by means of the protonic photometer and the Secchi disc (Clarke 1939a). Diatoms themselves may become sufficiently abundant to cause a significant decrease in transparency. The extent to which the plant cells may thus cut off their own light is shown by the relation between the Secchi disc measurements from eleven cruises to Georges Bank and the abundance of phytoplankton (Fig. 7). In all cases in which the plant pigments exceeded 40,000 Harvey Units per  $m^3$  the Secchi disc depth was found to be reduced to 8 m or less.

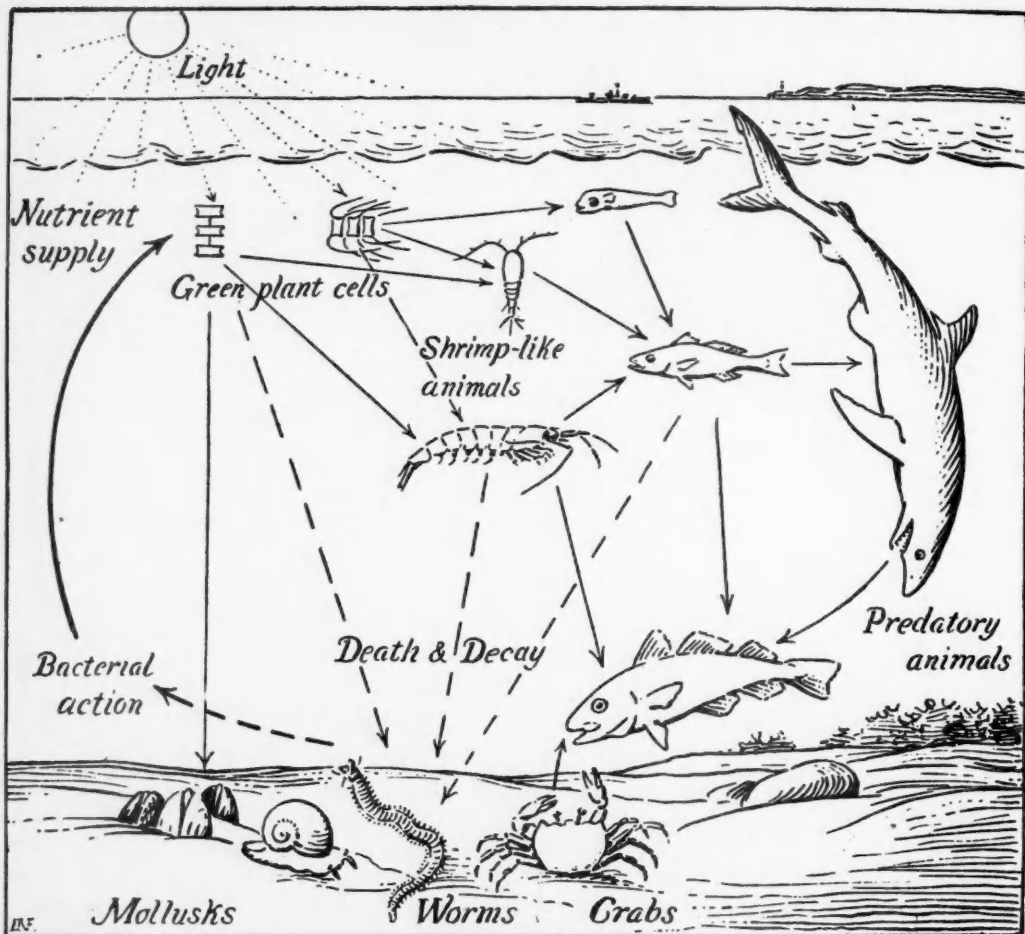


FIG. 6. Diagrammatic representation of the components of the production cycle in a marine area. (After Clarke, from "Science from Shipboard," Science Service, 1943.)

If we employ a value of  $.0017 \text{ g cal/cm}^2/\text{min}$  as an approximation for the compensation intensity<sup>2</sup> for marine diatoms (Jenkin 1937; Pettersson *et al.* 1934), we may calculate the maximum and minimum depths at which such an illumination would be found using the different transparencies found for the bank water and the various monthly averages for the light at the surface. If we assume that values based on the average illumination may be taken as rough approximations of the average position of the compensation point, the depths shown in the right hand columns of Table 1 give the limits down to which constructive plant growth can take place. Plant growth is thus clearly seen to be limited to a stratum far shallower than the depth of water over the main portion of Georges Bank. It is obvious that there would not be sufficient light to support

plants attached to the bottom except in the region of the Shoals and there the shifting sand would not permit attachment.

A second factor of concern in a marine area and one having especial importance on Georges Bank is the action of vertical mixing. Tidal currents over the bank prevent the water from becoming stratified even in summer and extensive vertical mixing takes place at all seasons. So complete is this process that there is little difference in temperature or salinity from surface to bottom over the whole of the central portion of the bank at any time during the year (Fig. 8). The turbulence of the bank water causes a vertical translocation of the diatoms which prevents their becoming adapted to any one condition of illumination and in addition carries them to levels below the compensation depth for a portion of the day. This harmful effect of vertical mixing on the utilization of light by the plant cells is perhaps counterbalanced to some extent by the

<sup>2</sup> The compensation intensity is the intensity of light at which the rate of photosynthesis is just equal to the rate of respiration. At illuminations below the compensation intensity no constructive growth of the plant cell can take place.

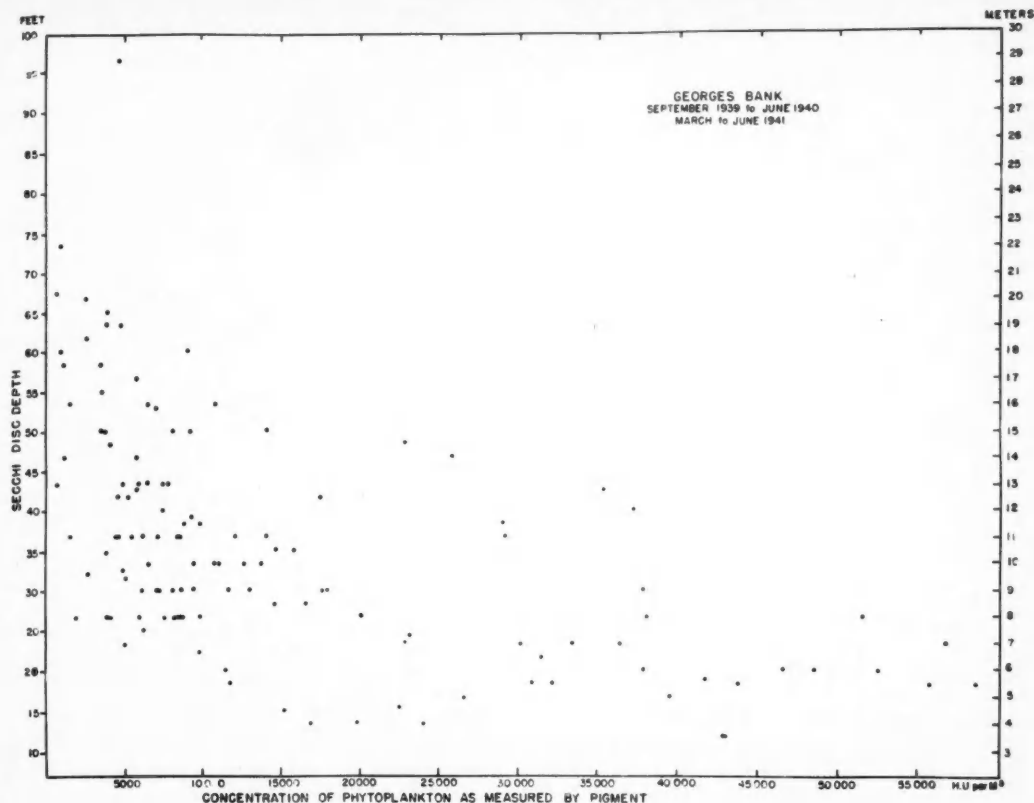


FIG. 7. Influence of phytoplankton abundance on the transparency of the water. Phytoplankton measured as Harvey Units per m<sup>3</sup> and transparency determined by Secchi disc depth (representing an average reduction of the illumination to 15% of its value at the surface).

action of the vertical movements in restoring water rich in nutrients to the upper layers. Little is known of the rate of this vertical transport for a situation such as Georges Bank and its measurement constitutes one of the most needed observations.

As far as our present information goes, it seems probable that the chief factor limiting the growth of the diatoms on Georges Bank during late autumn, winter, and early spring is the lack of sufficient illumination caused by the lower solar radiation and the higher degree of vertical turbulence. During the remainder of the year, when illumination is adequate, the lack of nutrients, the high temperature causing increased respiration, and the consumption by herbivores are considered to be the chief limiting factors (Riley, 1941b). The rate at which the herbivores consume the phytoplankton is difficult to determine but recent experiments and calculations strongly indicate that the grazing activity of copepods may constitute the chief agent for the reduction of the diatom population at times. (Fuller & Clarke 1936, Fuller 1937, Harvey 1937, Riley 1946).

The next step in the food cycle of a marine area

TABLE 1. Compensation Depths for Georges Bank.

Values for radiation are the average for each month (Sverdrup, Johnson, and Fleming, 1942, Table 25 after Kimball). Maximum and minimum Secchi disc depths are for all stations within the 200 m. contour; the average Secchi disc depths are for all stations within the central area of mixed water. The depths at which the compensation intensity (.0017 g. cal/cm<sup>2</sup>/min.) occurred were obtained from the Secchi disc depths, assuming the latter to represent a reduction of illumination to 15% (Clarke 1941).

Month	Incident Radiation g. cal/cm <sup>2</sup> /min.	Secchi Disc			Compensation Depth		
		Max. m.	Min. m.	Ave. m.	Max. m.	Min. m.	Ave. m.
January.....	.094	20	7	14	42	15	30
February.....	.135	..	..	..	..	..	..
March.....	.212	17	5.5	9	43	14	22
April.....	.272	8	3.5	5	21	9	14
May.....	.306	18	3.5	7	49	10	19
June.....	.329	22	4.5	11	59	12	30
July.....	.302	..	..	..	..	..	..
August.....	.267	..	..	..	..	..	..
September....	.230	18	6	8	47	15	21
October.....	.174	..	..	..	..	..	..
November.....	.115	..	..	..	..	..	..
December.....	.086	..	..	..	..	..	..

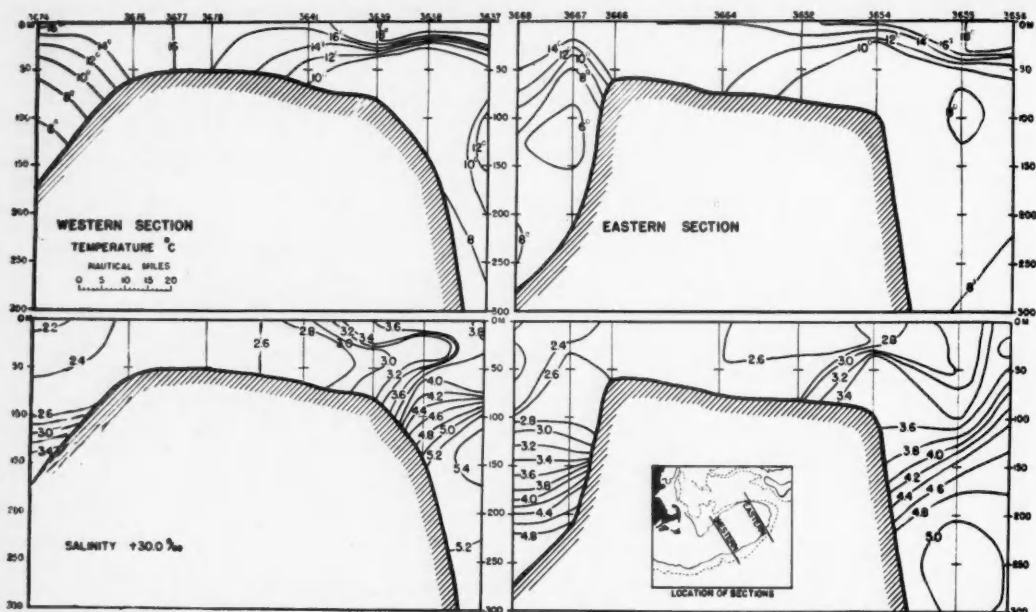


FIG. 8. Vertical sections showing the homogeneity of the water over Georges Bank. The contour of the bank is indicated by the crosshatching from the Gulf of Maine on the left to the edge of the Continental Shelf on the right. Station numbers for the cruise of September, 1939, appear at the top of the diagrams.

is the production of herbivores and we have seen that the copepods are the chief planktonic form at this trophic level on Georges Bank. It is obvious that the growth of the copepod population is dependent upon the availability, at the right time, of food which is of a suitable type and supplied in adequate amounts. Opinions differ, however, as to the nature and quantitative relations of the dependence of copepods upon diatoms (Clarke 1939e), and further investigation of these critical points is highly desirable. Values have been obtained for the seasonal increase and decrease in the standing crop of zooplankton on Georges Bank from our extensive surveys of the area, and for certain species the occurrence of reproductive periods has been determined (Clarke, Pierce, & Bumpus 1943). However, estimates of the food requirements of copepods based on laboratory tests vary widely, and we have little direct knowledge of the control of breeding and growth by the type and abundance of food. (Marshall, Nicholls, & Orr 1934, 1935; Clarke & Gellis 1935; Clarke & Bonnet 1939; Raymont & Gross 1942).

Another important influence controlling the abundance and the distribution of zooplankton is the action of horizontal currents. The bubble of mixed water overlying Georges Bank prevents the coastal current from sweeping across the bank and forces the water flowing out of the Gulf of Maine to circulate in a clockwise direction around the margin of the bank (Redfield, 1941). The mixed bank water, with its contained fauna and flora, thus tends to per-

sist with a certain degree of isolation. Outside water with different populations at times encroaches upon Georges Bank, and on other occasions segments of the bank water are drawn off, perhaps seriously decimating the communities of plants and animals which are dependent upon the bank environment (Walford 1939, Iselin 1939). A quantitative evaluation of the periods and amounts of these exchanges with the water beyond the margins of Georges Bank is seriously needed. The abundance of the plankton on the bank may be due in some cases both to accumulation brought about by currents and to an environment which is favorable for their vigorous growth. Such dual action has been clearly indicated in the control of the population of certain species of copepoda and sagittae (Clarke, Pierce, & Bumpus 1943).

It is certain that the benthos plays an important part in the food cycle of Georges Bank, since the cod and haddock, which bulk the largest in the commercial catch of fish, are bottom feeders. We have no quantitatively reliable information, however, on the size of the standing crop of the various components of the bottom fauna, to say nothing of their rates of production. This information is sorely needed. Another prominent category of animals, which appears to be partly associated with the bottom and partly pelagic, is composed of the larger planktonic crustacea. The biomass of these organisms has been found to average about half that represented by the smaller zooplankton, but in certain stages of their development and in certain areas they may become very abundant (Whiteley 1946). There



has been no opportunity as yet to ascertain what importance these larger crustacea may have in the food cycle of the bank.

Our knowledge of the quantitative relations of the fish at the top of the production pyramid is limited to statistics derived from the landings of commercial species. These data give us valuable information on the yield of fish from the area but knowledge of the standing crop and of the rates of production can be obtained only indirectly by means of calculations based on, as yet, unconfirmed assumptions.

Although there are so many vital gaps in our understanding of the various aspects of production in an area such as Georges Bank, it is desirable to bring together such data as have been obtained up to the present. The chief constituents and interdependencies of the ecological cycle on the bank, with approximate values representing our present knowledge of their quantitative relations, are shown schematically in Fig. 9. The diagram indicates that nutrients are provided by regeneration within the area but must also be brought into the area by currents, although the extent of this supply is not known. Currents also may bring in certain elements of the zooplankton and on occasion may account for an important loss of the permanent plankton, of the larvae of the benthos, and of the eggs and young stages of fish. A certain amount of migration of fish to and from the bank undoubtedly takes place, but our general knowledge of the fishery indicates that it is usually not important quantitatively.

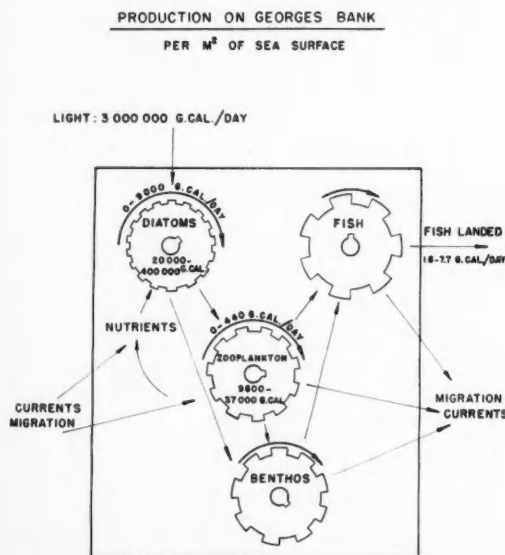


Fig. 9. Schematic representation of production on Georges Bank. The values given are the averages for the whole bank per square meter of sea surface. Maximum and minimum values within the cogwheels are for the standing crop, those over the wheels are for net production rate. Yield is indicated at right. For full explanation see text.

The maximum and minimum values for the average standing crop of diatoms and of zooplankton over the whole of Georges Bank have been calculated in terms of g cal. per square meter (Riley 1941b, Clarke 1939b) and are shown within the cogwheels in the diagram. One cc. of zooplankton was found to be equal to 1 g wet weight or 0.1 g dry weight, and equivalent to 400 g cal of energy. Adequate quantitative data exist neither for the abundance nor growth of the benthos. For the fish, however, estimates based on the landings and recruitment of the haddock (which usually comprise the major portion of the commercial catch) during the early 1930's suggest that the standing crop of market-sized fish at the beginning of the year might be no greater than twice the amount of the landings during the year (W. C. Herrington, private communication.)

The rates of net production are indicated schematically in the diagram as the rates at which the cogwheels are turning. In the case of the diatoms (Riley 1941b) and zooplankton<sup>3</sup> the rates vary from zero during the months of the year when no growth is taking place, to the approximate maximum values shown (averages for the whole bank). In the absence of actual data on the growth rates of the fish, the average daily value for the fish landed during the whole year may be used as a very rough minimum value for net production.

This preliminary picture for Georges Bank indicates a pyramid of abundance and a pyramid of production rates which diminish sharply toward the higher trophic levels. According to these very approximate values, the 3 million g cal of energy which fall on each square meter of sea surface per day on Georges Bank, as an average for the year, would be used by the diatoms with a maximum efficiency of about 0.3%. The production of zooplankton represents a maximum efficiency of about 0.015%.

The low value for the efficiency of the production of phytoplankton in a marine area is due in part to the inefficiency of the process of photosynthesis itself and in part to the fact that only a small fraction of the light incident on the sea surface can be absorbed by the plant cells because a large part of the radiation is removed by the water medium. Fresh-water phytoplankton has been found by Manning to produce carbohydrate under natural conditions with an average efficiency of 2.7% of the light absorbed (Clarke 1939a). Since in a series of Wisconsin lakes only 1.6% to 14% of the light incident on the lake was absorbed by the plant cells, the over-all efficiency of gross plant production in the utilization of solar energy ranged from 0.043% to 0.38% in these cases. In Long Island Sound the efficiency of gross plant production appeared to be about 0.55% to 0.82% and the estimated mean efficiency of net plant production was 0.31% (Riley 1941a). These values are in satisfactory agreement

<sup>3</sup> Clarke (Unpublished data). A value for the maximum production rate of the zooplankton was approximated by finding the average daily increment in the standing crop for the period of most rapid growth (April).

with the corresponding determinations for Georges Bank (Riley 1941b).

It is of interest to compare the foregoing calculations with similar determinations undertaken for terrestrial plants. Plants on land enjoy the initial advantage that they can absorb the major portion of the incident radiation when the vegetation completely covers the ground. Values for the production of various types of the earth's vegetation have been summarized by Riley (1944) with an estimate for the average yearly efficiency of gross production for terrestrial plants of about 0.09%, and a maximum value, obtained in the best forests, of about 0.25% (Krogh 1934). When the calculations are limited to the growing season, higher efficiencies are to be expected. Corn grown for 100 days in Ohio under the best conditions produced a dry weight of 13,200 lbs./acre for the whole plants, or 4,750 lbs./acre for the grain alone, representing a maximum yield of 100 bushels of grain per acre (Transeau 1926). When the respiration loss is added, the former value is equivalent to a gross production of 74,000 g cal/m<sup>2</sup>/day, or an efficiency for gross plant production of 1.6%, and for net plant production of 1.2%. These efficiencies are noticeably higher than the maximum observed on Georges Bank.

The weight of whole fish of all species landed annually from Georges Bank (area about 10 million acres) from 1923 to 1945 ranged from a minimum of 63 million lbs. in 1934 to a maximum of 289 million lbs. in 1929. This represents a yield of 7 to 33 lbs./acre/year, which is equivalent to 1.6 to 7.7 g cal/m<sup>2</sup>/day (assuming an energy content of 740 g cal/g for raw, fresh fish)<sup>4</sup> or an efficiency of utilization of the average incident radiation of .00005% to .00025%. This yield is similar to that of 19 lbs./acre/year calculated by Juday (1940) for Lake Mendota but is considerably less than values for the animal products of cultivated land which may give yields for cattle and sheep of 150 lbs./acre/year (Graham 1944). The fact that cattle and sheep are herbivorous animals with only two links in their food chain, gives them an advantage over commercial species of fish which may be secondary or tertiary carnivores. Fertilized fresh-water ponds in the Southeast will support a standing crop of about 600 lbs. of fish per acre and will give a yield of about 300 lbs./acre/year. (Swingle & Smith 1941, 1942).

If the dynamics of production in a marine area result in an efficiency which seems discouragingly low, it should nevertheless be borne in mind that for an area like Georges Bank man is required to expend no effort in cultivation and that renewed fertilization is automatically provided. Thus if the bank is exploited intelligently, it can provide a valuable crop for an indefinite period.

<sup>4</sup>Taken from the table of Composition and Value of Food in the Handbook of Chemistry and Physics. Chemical Rubber Publishing Co., 1944, p. 1458.

## SUMMARY

A consideration of the productivity of a natural area should involve the concepts of (1) standing crop, (2) material removed, including the yield to man, and (3) the production rate. The production rate of the organisms at different trophic levels should be considered separately and distinction made between gross production (assimilation), net production (growth), and net increase in the standing crop per unit time. Diagrams are presented illustrating the interrelations between the processes of production, consumption, and decomposition at the various levels in the ecological complex.

The application of the foregoing concepts to a marine area is illustrated using data from Georges Bank. The nature of the fundamental factors underlying the productivity of the bank is pointed out with a consideration of the quantitative relationships insofar as the existing measurements permit. Values for the standing crop and for the net production of the phytoplankton and the zooplankton are presented with a discussion of the controlling influence of the reduction of light in the water and of the displacements due to currents. Values for the yield of the commercial catch of fish from the bank are compared with yields obtained from fresh-water and terrestrial areas.

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## APPENDIX

### MATHEMATICAL FORMULATION OF BIOLOGICAL PRODUCTIVITY

G. L. CLARKE, W. T. EDMONDSON, & W. E. RICKER

The foregoing consideration of production rate may be expressed quantitatively in general mathematical terms.\* The advantage of such treatment is that the relationships of the various concepts and rates discussed are emphasized, and it is made clear just what quantities are of importance in studies of production. The rates of production may be expressed by a series of simple differential equations:

$$\frac{dP}{dt}^1 = A \cdot P \quad \text{Gross Production Rate (1)}$$

$$\frac{dP}{dt}^2 = (A - R) \cdot P \quad \text{Net Production Rate (2)}$$

$$\frac{dP}{dt}^3 = (A - R - D - C) \cdot P \quad \text{Net Rate of Increase or Decrease (3)}$$

where:

- A = rate of assimilation per unit of population
- R = rate of respiration per unit of population
- D = rate of decomposition per unit of population
- C = rate of consumption per unit of population
- P = standing crop.

The assumption indicated by these expressions is that the assimilation, etc. per unit area (or volume) is proportional to the standing crop. This is probably true over a wide range of density, but as soon as the population reaches the density where harmful effects of crowding become discernible, the relationship changes. In practical terms this means that for any given set of conditions, the corresponding mean values of A, R etc. would be taken. In addition, it should be noted that the use of these equations in describing populations is limited to one given taxonomic unit or trophic level at a time. In work on natural phytoplankton populations, A and R can be estimated by means of black and clear bottle experiments. If P is determined at close intervals, the net rate of change (3) can be found, and from these data an estimate made of the sum of D and C. Knowing A, R, and P, we can determine the total amount of material or energy entering a population during a period of time (10), and the amount which was left after respiration, which is that added to the population.

If the rate of assimilation is greater than the sum

of the destructive rates, new organisms will be formed at the rate indicated. The amount of material which would theoretically exist at the end of a period of time,  $t$ , would be given by integrations of the first three equations. These are given for the assimilative process alone, and for this process diminished by the several destructive processes:

$$P_1(t) = P_0 e^{At} \quad (4)$$

$$P_2(t) = P_0 e^{(A-R)t} \quad (5)$$

$$P_3(t) = P_0 e^{(A-R-D-C)t} \quad (6)$$

where:

- $P_0$  = standing crop at beginning of period
- $P_t$  = standing crop at end of period

Equation 5 gives the potential standing crop at the end of the period if the population grew at the rate (A-R) with no predation or other death. Equation 4 by analogy gives the potential crop if catabolism had been suspended, and this is of hypothetical interest only. Equation 6 is descriptive of the situation in real populations as it takes account of the death of material. The amounts theoretically formed during the interval by  $P_0$  are given by

$$P_1(t) - P_0 = \text{Potential Gross Production for Period, } t. \quad (7)$$

$$P_2(t) - P_0 = \text{Potential Net Production for Period, } t. \quad (8)$$

$$P_3(t) - P_0 = \text{Net Increase (or Decrease) for Period, } t. \quad (9)$$

The assumption made in establishing equations (1) to (3) leads to the exponential growth of the population shown in equations (4) to (6). This is valid for an unlimited environment, but for a more complete description it is necessary to include an expression for decreasing growth rate at high densities, and this leads to the well-known logistic equation. A case in which the grazing animal reproduces so fast relative to the food organism that the total grazing intensity becomes greater than the production of the food organism has been treated by Fleming (1939).

In actual populations, the material which is lost

\*The authors wish to acknowledge suggestions made by Dr. G. A. Riley, who has also presented mathematical treatments of similar considerations of productivity (Riley 1941b, 1946).

in catabolism and to predators is not available for reproducing the population. Therefore, the amount of material or energy incorporated into new elements of the population will be less than that indicated above if there is any such loss. The actual amount formed during the period,  $t$ , may be expressed simply as the product of the rate times the mean standing crop and length of time:

$$t \cdot \bar{P} \cdot A \quad \text{Actual Gross Production during period, } t \quad (10)$$

$$t \cdot \bar{P} \cdot (A - R) \quad \text{Actual Net Production during period, } t \quad (11)$$

$$t \cdot \bar{P} \cdot (A - R - D - C) \quad \text{Actual Net Increase (or Decrease) in Standing Crop during period, } t \quad (12)$$

where  $\bar{P}$  is the mean standing crop during the period (cf. Ricker, 1945). This quantity can be obtained, in practical work, simply by averaging the determinations of standing crop during the period. Since population growth is not linear, the determinations should be frequently made. The exact value of  $\bar{P}$  during any interval is given by the following expression:

$$\bar{P} = \frac{P_0(e^{(A-R-D-C)t} - 1)}{t(A-R-D-C)} \quad (13)$$

The derivation of this expression is as follows. Equation (6) describes a curve which represents the growth of the population. Integrating equation (6)

gives the area under the curve between the time limits taken, and dividing this by the length of time,  $t$ , gives the mean value of the ordinate, or mean standing crop. Equation (13) represents the integration of equation (6) divided by  $t$  and thus gives the value of the average standing crop.

Rate of production as defined by equations (1) to (3), and amount of production over a period of time as defined by equations (10) to (12), may be expressed in terms of energy or of the mass of any constituent of the organisms which is reasonable to use, such as carbon. The equations give production in terms of mass or abundance in whatever units are used for expressing population density. If  $\bar{P}$  is divided into equations (10) to (12), the result is in terms of material produced per unit of population. Equation (10) defines the amount of material (or energy) entering the population regardless of what happens to it subsequently. Equation (11) defines how much of that material is left after respiration has removed a portion of it. The amount respired would be defined by

$$t \cdot \bar{P} \cdot R \quad (14)$$

Equation (12) defines how much material is left in the standing crop after losses by death are considered. Equation (12) becomes identical with (9) when the value for  $\bar{P}$  is substituted. The considerations outlined here are capable of considerable development and offer a profitable field of investigation for ecologists.





THE DYNAMICS OF FRESH-WATER PLANKTON  
POPULATIONS

ROBERT W. PENNAK  
*Biology Department, University of Colorado*

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# THE DYNAMICS OF FRESH-WATER PLANKTON POPULATIONS\*

## INTRODUCTION

In this brief outline of the basic principles of the dynamics of fresh-water plankton populations, we shall attempt to answer five fundamental questions: (1) What is the general composition of the fresh-water plankton? (2) What are the nutritional interrelationships of these organisms? (3) What is the nature of seasonal and annual variations in plankton populations? (4) What are the probable ecological factors responsible for these variations? (5) How may plankton production be measured? To questions (1) and (3) we have reasonably satisfactory answers; to question (5) we can offer a partial answer; and to questions (2) and (4) we can only suggest inadequate answers, confess our ignorance, and express the hope that future research will fill these gaps in our knowledge.

## GENERAL COMPOSITION

We shall use the word "plankton" in its broadest sense, including all organisms, both plant and animal, which are suspended in the water and are not independent of water movements. From the standpoint of their biotic roles in the open waters of a lake or stream, these organisms comprise three familiar groups: (1) the zooplankton, including the Cladocera (water fleas), Copepoda, Rotatoria (rotifers), Protozoa, and a very few limnetic insect larvae; (2) the true photosynthetic phytoplankton, or algae, including the Bacillarieae (diatoms), Myxophyceae (blue-green algae), Chlorophyceae (green algae), and a few other classes of less significance; and (3) non-photosynthetic plants, including the Schizomycetes (true bacteria) and Phycomycetes (aquatic fungi). In any plankton population there are unicellular flagellates which possess both plant and animal characteristics and which a botanist classifies as plants, and a zoologist as animals. Although some of these forms are mainly holophytic, many are mixotrophic, and for the sake of convenience they are here all treated as Protozoa along with other flagellates, ciliates, and amoeboid forms. A few of the more familiar of these genera of controversial affinities are Ceratium, Dinobryon, Eudorina, Peridinium, and Trachelomonas.

If regular weekly or monthly plankton samples are taken at an open water station in a river or lake throughout the year, one can expect to identify from 40 to 150 species of algae and 25 to 100 species

of zooplankters. The great majority of these species will be uncommon or rare, occurring in only one to several samples. A few, however, will be abundant and common during much or most of the year. A single haul of the net or a single plankton trap catch on any particular day will usually be found to have taken ten or less species of phytoplankters which are abundant and ten or less species of zooplankters which are abundant. The latter group will almost invariably contain two to four species of Entomostraca (usually *Daphnia*, *Cyclops*, and/or *Diaptomus*), two to six species of rotifers, and two to four Protozoa.

The number of individual plankters occurring in lakes and streams at any moment is, as we shall see, highly variable, but usually the algae number in the hundreds of thousands to tens of millions of cells per liter, the Protozoa in thousands to hundreds of thousands of individuals per liter, and the Rotatoria and Entomostraca in tens to hundreds per liter.

The total weight of all of the particulate materials in fresh waters, including both living organisms and detritus, usually ranges between 0.3 and 10.0 milligrams per liter (dry weight). From 20 to 80 per cent or more of this quantity is composed of detritus, including dead and disintegrating plankters. The weight of the bacteria and molds is negligible, but the total mass of the living green phytoplankton is usually two to ten times as great as the mass of the zooplankton.

## NUTRITIONAL INTERRELATIONSHIPS

As indicated in Figure 1, the fundamental interrelationships between the various groups of plankton organisms are primarily nutritional in character. The phytoplankters have been collectively called the "producers," the zooplankters "consumers," and the bacteria and molds "transformers." Materials are lost from this cycle in three chief ways. First, the grazing activities of small fish remove zooplankton, phytoplankton, and, incidentally, some bacteria, molds, and detritus, and convert them into protoplasm at a higher trophic level. The fraction of the plankton which may be removed by small fish in fresh-water environments is a problem about which almost nothing is known. With reference to the total plankton mass, however, it seems likely that only a small to insignificant fraction is usually lost in this way; this is unquestionably true of lakes with small populations of plankton-feeding fish. Second, an additional insignificant amount of living plankton is consumed by the invertebrate predators and browsers of the bottom fauna. Third, when plankton organisms die and become a part of the particulate detri-

\* Contribution No. 12, Limnology Laboratory, Department of Biology, University of Colorado. Field and laboratory work on Colorado lakes was made possible through grants from the Penrose Fund of the American Philosophical Society and the University of Colorado Research Fund. The author is most grateful for such assistance.

tus, some of them sink to the bottom. There they may be consumed sooner or later by the bottom fauna, acted upon by bacteria, and incorporated into the more or less inert bottom deposits. In the last event, a fraction is permanently lost from the lake so far as plankton nutrition is concerned.

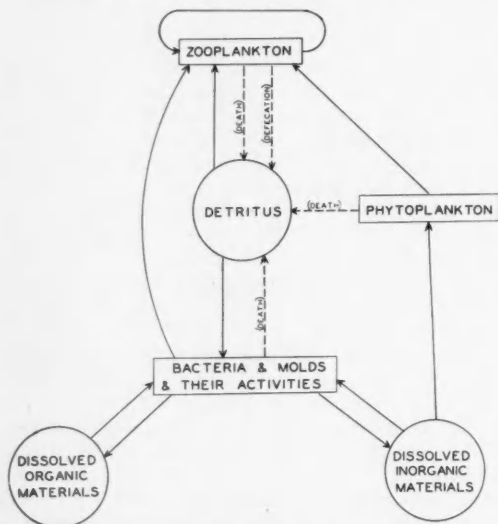


FIG. 1. Important nutritional interrelationships in the plankton ecosystem.

The nutritive materials lost from the plankton environment are being continuously replaced and returned to the water by bacterial action in the bottom deposits, by algal photosynthesis and further anabolism, and by the addition of organic and inorganic materials brought into the water by rains and streams and blown in by winds.

Aside from these matters of income and outgo, we regard the plankton as a definite, but constantly changing, dynamic, biotic community, complete within itself, and because this community and its activities are so inextricably associated with detritus and dissolved nutrients, we may even go so far as to consider the whole as an *ecosystem*.

Just as in terrestrial environments, all [the] flesh [of the plankton ecosystem] is grass, the primary source of zooplankton protoplasm residing ultimately in the photosynthetic process and in the further synthesis of more complex carbohydrates, fats, and proteins by algae (and perhaps by some autotrophic bacteria).

In addition to phytoplankton, detritus, and bacteria as food sources (Fig. 1), the zooplankton derives some food from itself; small rotifers are eaten by large copepods, for example, and protozoa are eaten regularly by both Entomostraca and rotifers, both of these groups being essentially omnivorous.

Hydrobiologists are becoming increasingly aware of the supreme significance of aquatic bacteria and

their physiological activities in the plankton ecosystem. Although these bacteria constitute a characteristic autochthonous flora in natural unpolluted waters, they are largely an unknown flora and are exceedingly difficult to enumerate and study. Plate counts, direct counts, enumeration of bacteria deposited on submerged glass slides, and the use of dilution series and selective media all have disadvantages. Furthermore, the ordinary nutrients and methods of culturing bacteria in the laboratory are inadequate so far as the flora of lakes and streams is concerned. A range of 10° to 25° C. seems to be most favorable for their growth.

Bacteria are always present at all depths, but the vertical and seasonal distribution are highly variable and often unexplainable. In most lake waters their numbers range between 1,000 and 2,000,000 per cubic centimeter. Usually the number is proportional to the amount of organic and inorganic matter present in the water, but there are numerous exceptions. Many are periphytic and attached to the surface of plankters and bits of detritus.

All important physiological groups present in soils occur also in lakes and streams, and aside from their importance in utilizing dissolved materials in building up their own protoplasm and serving as food for zooplankton, they are essential to the plankton ecosystem as *chemical transformers*. Briefly, this process involves the decomposition of complex dead organic matter by heterotrophic bacteria into simple compounds, followed by oxidation and mineralization of these compounds by autotrophic bacteria, so that essential elements are again available (as phosphates, nitrates, sulphates, and bicarbonates, for example) for the synthesis of new organic matter by algae. Thus the aquatic bacteria link the ends of a food chain, making it a cycle.

In addition to the chemosynthetic autotrophic bacteria, natural waters also contain photosynthetic species, the red, purple, and green sulphur bacteria, which have pigments that absorb light energy and use it to transform carbon dioxide and hydrogen sulphide into organic compounds. The relative significance of these bacteria in the economy of the plankton ecosystem is unknown.

Recently Weston (1941) has called attention to the fact that aquatic Phycomycetes probably play an important, though relatively unknown, role in lake waters, comparable to that played by heterotrophic bacteria.

#### ANNUAL AND SEASONAL CYCLES

In studying the interrelationships of the plankton ecosystem, it is logical that we should be concerned with the annual and seasonal cycles of abundance and the probable factors responsible for these numerical variations. Figure 2 is a diagrammatic representation of the widely accepted concept of the annual plankton curve in typical medium to large lakes and rivers in temperate latitudes. The months of the year are indicated horizontally, and weight or numbers of organisms per unit volume or area are indi-



eated vertically. Briefly, this curve shows a large spring pulse, a decreased population during the summer, a second, less pronounced, pulse in the autumn, and a very small population during the winter. The zooplankton and phytoplankton pulses are generally considered to be coincident or immediately following each other. In some instances either or both of the two main pulses are relatively much more or much less conspicuous than indicated. Also, the peak of each pulse may be earlier or later by as much as six weeks.

The smoothed curve of Figure 2 is actually a composite of many short, long, low, and high curves, one for each of the numerous species of phytoplankton and zooplankton, and although it is not the concern of the present paper to consider populations of individual species, it should be emphasized that the seasons of maximum and minimum abundance are usually thought to be more or less distinct for each species. Eddy (1934) has accordingly classified plankters as hiemal, vernal, estival, serotinal, incidental, and perennial species. Nevertheless, the expected periodicity of a species present in a lake or stream is often greatly modified, exaggerated, suppressed, or even eliminated by the combined effects of the physical, chemical, and biological conditions obtaining at a particular time in each body of water.

With reference to the phytoplankton, it is usually stated that diatoms, as a whole, are most abundant

in spring and autumn, blue-green algae in late summer and early autumn, and greens in midsummer. The total Entomostraca curve generally is said to follow the typical bimodal annual curve, while the cyclic occurrence of total rotifers and protozoa is more irregular, depending partially on the particular species present. Characteristically, these two latter groups are not abundant during the cold months.

If one examines the plankton literature carefully, he will soon discover a paucity of publications containing extensive, *year-round, quantitative* data for both phytoplankton and zooplankton populations, and that the classical curve shown in Figure 2 is actually based on material from a very few medium to large and relatively deep lakes and rivers. Some of the more important of these few extensive papers are those of Kofoid (1908), Allen (1920), Birge & Juday (1922), Riley (1940), and Chandler (1940).

With these facts in mind, the present writer made year-round quantitative studies of both the phytoplankton and zooplankton of seven typical, but widely differing, northern Colorado lakes between 1940 and 1942. These lakes are all small, shallow, with symmetrical basins, with areas ranging from 4.9 to 42.8 hectares, and with mean depths of 1.8 to 6.5 meters. One of them had sharp temperature stratification during the summer, and five had pronounced oxygen stratification. Zooplankton samples were taken at monthly intervals at four to six evenly

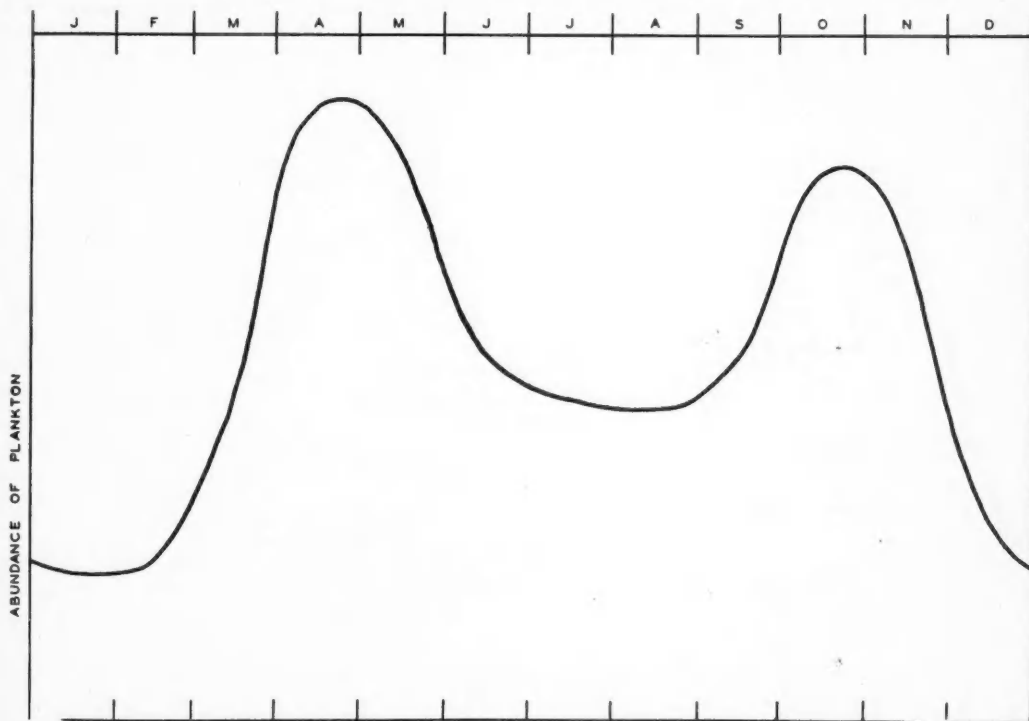


FIG. 2. Annual variations of the total plankton population in large, deep lakes (diagrammatic).

spaced depths from surface to bottom at the deepest point in each lake with a ten-liter plankton trap, and phytoplankton determinations were made for the corresponding depths by running 500 cc. samples through a Foerst plankton centrifuge. The results were calculated as mean numbers of phytoplankton cells and individual zooplankters per liter for each day a particular lake was visited. Some of these data have been summarized in Figures 3 to 6 and afford interesting comparisons with the schematic curve of Figure 2.

In Figure 3, for example, the seasonal duration of the phytoplankton and protozoa pulses are indicated for each of these lakes, a pulse being arbitrarily considered as any population which is twice or more as great as the mean annual population. It is easily seen that only two of the seven lakes showed any indication of spring and autumn diatom pulses; none of them showed late summer and early autumn pulses of blue-green algae; and only two had mid-summer pulses of greens. None of these data should be confused with the tremendous "nuisance blooms" which occur in the summer months in some lakes.

All of the phytoplankton data are combined to show total numbers of cells per liter throughout the year in Figure 4. The most striking feature of this

figure is, of course, the tremendous differences in the algal populations of these lakes. Only in Boulder Lake, however, were there characteristic spring and autumn pulses. Gaynor Lake had three great pulses—one in spring, one in midsummer, and one in autumn. Beasley Reservoir had pulses in winter, summer, and autumn. Each of the other four lakes had only a single peak in the annual population curve; in three of these it occurred sometime during the spring, and in the other during the summer.

Both the total protozoa (Fig. 3) and rotifer populations (Fig. 5) were in accordance with the widely accepted notions that the numbers of these organisms are highly variable, that there are no definite seasonal pulses, and that they are least abundant during the winter months.

Irregular results are also shown for the Cladocera populations in Figure 6. Only one of the seven curves, Boulder Lake, shows clear cut spring and autumn maxima. Allens Lake has a suggestion of spring and autumn maxima, but all of the other curves have two maxima at various other times of the year, or a single maximum, or three maxima.

Comparable curves for the Copepoda (not figured) are even more varied, none of the seven lakes having spring and autumn maxima.

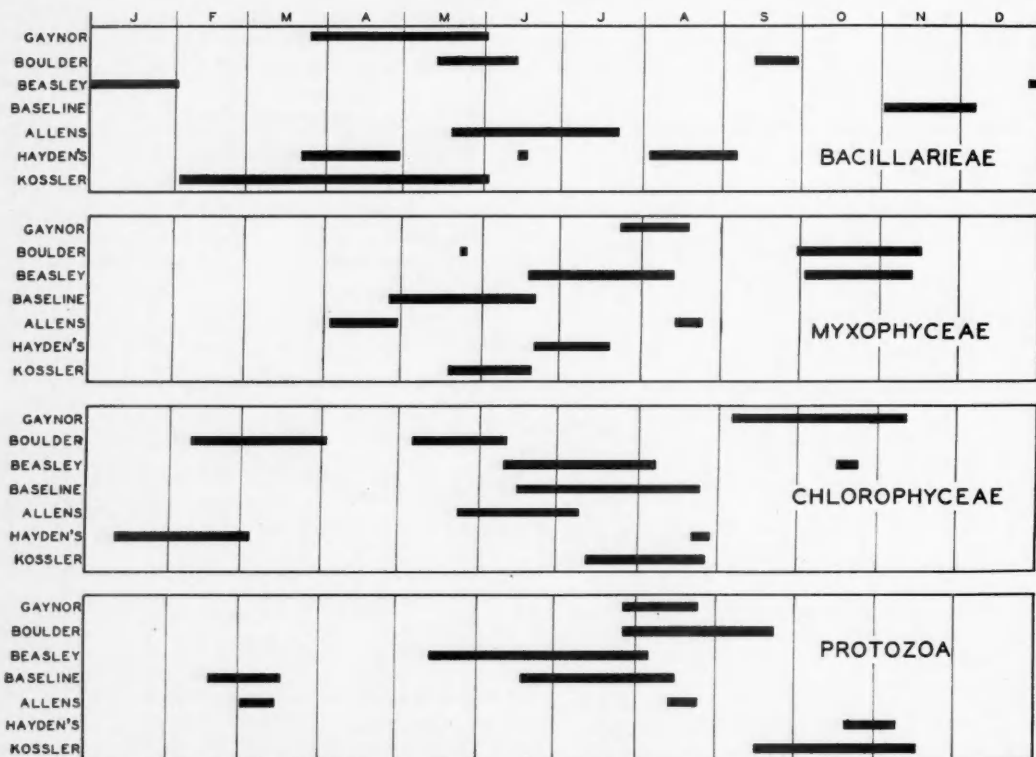


FIG. 3. Seasonal pulses of Bacillariaceae, Myxophyceae, Chlorophyceae, and Protozoa in seven northern Colorado lakes. A pulse is arbitrarily considered to be any average population for all depths which is twice or more as great as the mean annual standing crop.

The basic conclusion which might be drawn from such inconsistent results is self evident. Personally, the present writer has little faith left in the idea of definite seasonal pulses for the major groups of algae, or of total phytoplankton and Entomostraca pulses in spring and fall, except as these may occur in certain larger and deeper lakes. From the standpoint of the seven Colorado lakes, there may be one, two, three, or no pulses, and these may occur at almost any time of the year.

A detailed discussion of the ecological factors responsible for such a wide variation of plankton population curves in small as compared with medium to large lakes is, of course, beyond the scope of this brief outline. A few pertinent suggestions will be made, however, in the section which follows, and a detailed analysis of conditions in each of the seven Colorado lakes will appear in another publication. Nevertheless, judging from these data and from other unpublished data in possession of the writer, annual and seasonal cycles seem to be of a highly variable nature from lake to lake and from year to year within the same lake. The whole picture emphasizes again the fact that each body of water is distinctive

and should be meticulously studied as an individual case.

Like so many other ecological problems dealing with communities, the study of plankton cycles, competition, predation, and associated phenomena resolves itself into a careful investigation of the ecological requirements of *individual species* under *natural conditions*, supplemented by carefully controlled laboratory work. In our estimation, such studies on single species and analyses of causes and effects could be much more profitably pursued on a group of small lakes representing a wide variety of ecological conditions and plankton populations than on a group of large and less dissimilar bodies of water.

#### FACTORS AFFECTING PLANKTON ABUNDANCE

As recently as 20 years ago it was widely held that plankton populations were controlled, quantitatively and qualitatively, by some one or several obvious environmental factors, such as pH, oxygen, carbon dioxide, nitrates, and temperature. As more and more work has been done, however, it has be-

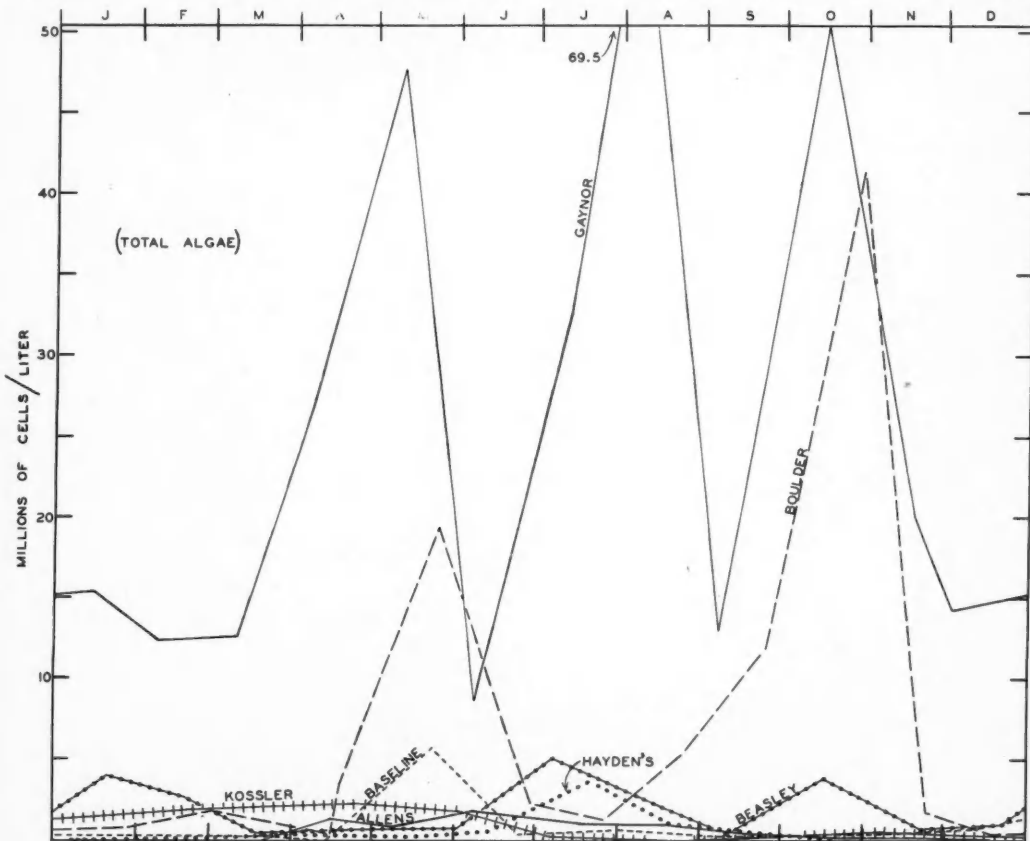


FIG. 4. Annual population cycles of total algae in seven northern Colorado lakes. Each point on the curves represents an average population for several depths between surface and bottom on a particular day.

come apparent that the plankton ecosystem is far more complicated than most earlier workers had imagined, and that factors previously regarded as limiting factors in themselves are now regarded as being of little importance. Present tendencies are directed toward the study of the interaction of many factors with special emphasis on some of the less obvious and less easily measured factors, such as the probable significance of "trace" elements and biochemical relationships between organisms.

A thorough discussion of our present knowledge of the environmental factors affecting plankton abundance is beyond the scope of this brief review, but we shall summarize, in outline form, some of the more important aspects of this problem and indicate some lines of investigation which might lead to fruitful conclusions.

#### CHEMICAL FACTORS

1. In the broad sense, there are greater numbers of zooplankton and phytoplankton organisms where there are larger total quantities of dissolved nutrients. Most of us, for example, are familiar with the quantitative plankton distinctions between "hard-water" and "soft-water" lakes. The basic truth of

the principle has been demonstrated many times by investigators who have rapidly increased the plankton production of small ponds as much as 50 to 200 per cent or more by the addition of commercial and natural fertilizers, and it is well known that sewage effluents greatly increase the plankton of lakes and rivers. It should be strongly emphasized, however, that this quantitative nutrient principle is true only in a general way and within ordinary limits; the correlation is not direct, and there are many exceptions.

2. Qualitatively, the composition of the plankton may be largely determined not by the total quantity of dissolved materials, but by the smallest quantity of an ion or compound which may be a limiting factor for each species. This problem is extremely complicated, and, as Hutchinson (1944) has said: "Clear cut correlations between chemical conditions and the qualitative composition of the phytoplankton [and zooplankton] are not to be expected."

3. In most lakes and streams nearly all inorganic nutrients appear to be present in excess, even though these substances may occur in surprisingly small quantities. A concentration of only a milli-

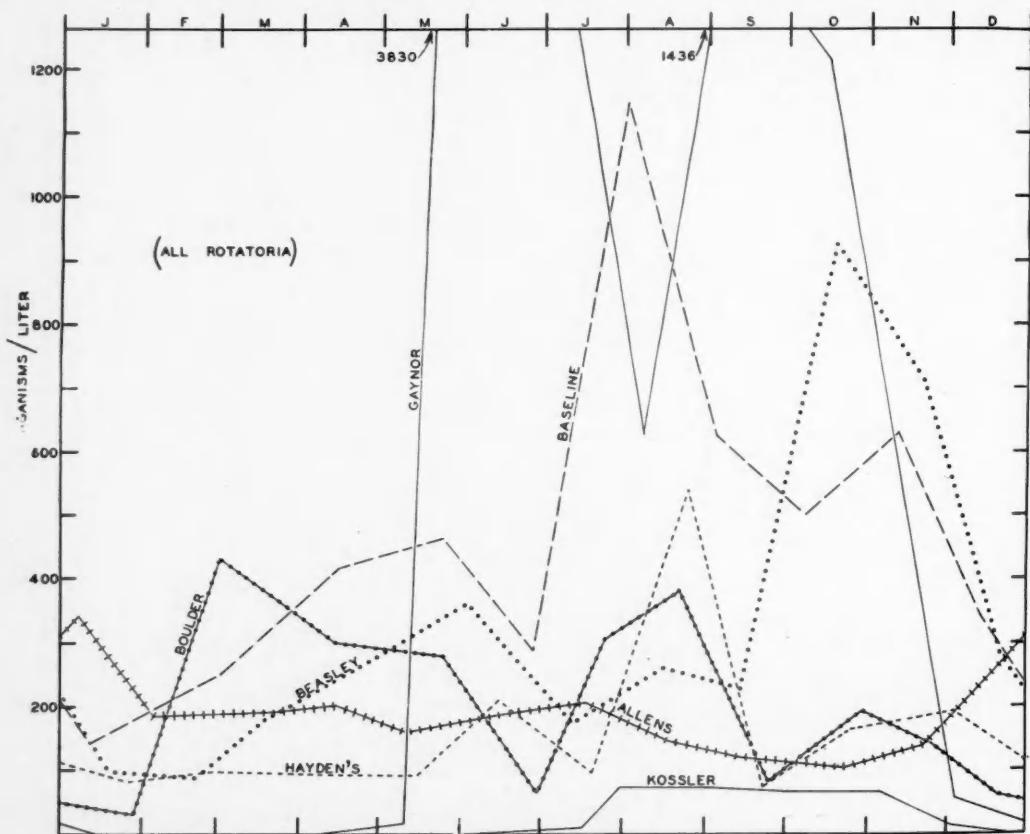


FIG. 5. Annual population cycles of total Rotatoria in seven northern Colorado lakes. Each point on the curves represents an average population for several depths between surface and bottom on a particular day.

gram or two per liter usually seems to be ample for such substances as silicon, magnesium, calcium, chlorine, potassium, and sodium.

4. The ratios of some ions may determine the qualitative and quantitative nature of the plankton. Waters having low sodium-potassium: calcium-magnesium ratios, for example, are characterized by diatom and blue-green algae floras, while those with high ratios usually have a predominant Chlorophyceae flora (Prescott 1939). We hope that our temptation to speculate further along these lines will be justified by more research and specific evidence.

5. The two ions most commonly cited as limiting factors for phytoplankton growth are nitrate nitrogen and phosphate phosphorus. The former is present in most surface waters in quantities ranging between 0.002 and 0.200 milligrams per liter, and the latter between 0.002 and 0.020 milligrams per liter. Phosphorus is considered to be the limiting factor much more frequently than nitrogen, even though the range of 0.002 to 0.005 milligrams per liter includes lake waters of very low to high productivity! It is, of course, exceedingly difficult to demonstrate the effects of these substances as limiting factors directly, to the exclusion of all other factors. With reference to the production of tremendous summer algal blooms in certain lakes (as distinct from ordinary pulses), Mead *et al.* (1945) conclude that inorganic nitrogen may be "a limiting factor in regard to the amount of growth which could be produced and the inorganic phosphorus acting largely as a governor upon the rate at which growths occurred." Chu (1943) has shown that the upper limits of nitrogen and phosphorus for opti-

mum growth of several common genera of phytoplankton never occur in natural waters.

6. The pronounced plankton pulses in the spring and fall in larger lakes are often said to be due to the enrichment of waters at all depths with plant nutrients which have settled into the lower waters during the preceding periods of stagnation. Within the past ten years, however, data have been presented which show that in many instances a good supply of nutrients remains in the epilimnion throughout periods of stagnation so that they cannot, in themselves, be limiting factors. The fact that pronounced pulses occur in spring and/or autumn, as well as in summer, in Colorado lakes which remain essentially in complete circulation throughout the year is further evidence that nutrients are only a part of the story. Undoubtedly such factors as light and temperature play important accessory roles.

7. "Trace" elements may be of great importance in plankton environments for certain species. Guseva (1939), for example, has shown that concentrations of more than 0.2 milligrams of manganese per liter are definitely toxic to some plankters. Other workers have found that copper may accumulate in the hypolimnion during the summer in sufficient quantities to be toxic. Hutchinson (1932) believes that the high zinc content (0.65 milligrams per liter) is toxic and prevents the occurrence of Cladocera in Bear Lake, Idaho.

8. The usual range of total dissolved organic matter in fresh waters is 3 to 60 milligrams per liter (dry weight). This quantity remains remarkably constant throughout the year and amounts to four to eight times the weight of the total plankton and

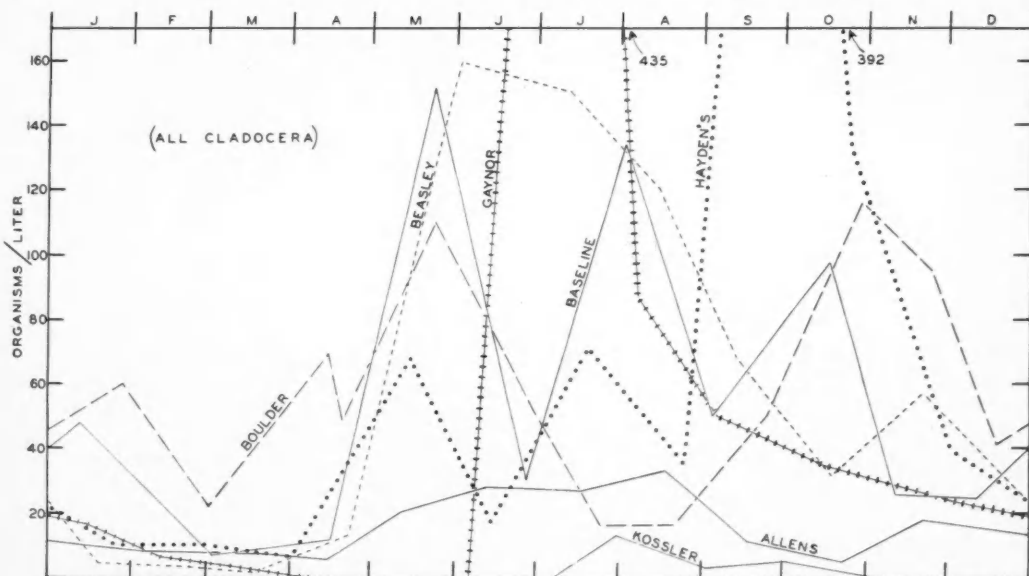


FIG. 6. Annual population cycles of total Cladocera in seven northern Colorado lakes. Each point on the curves represents an average population for several depths between surface and bottom on a particular day.



detritus. The real significance of the dissolved organic matter is an unknown and intriguing problem, but the realization is slowly gaining favor that one of our most fruitful sources of information concerning the dynamics of plankton populations may eventually lie in the study of some of the many organic compounds in this complex. These accessory organic substances may possibly be excretory materials, disintegration products, and intermediate metabolic products which are capable of acting as growth promoters or growth inhibitors for certain species; perhaps they are necessary for some of the intermediate roles played by the bacteria in the plankton cycle. It is interesting to note that Juday (1942) found that the addition of organic fertilizers to Weber Lake, Wisconsin, greatly increased the plankton crop, while inorganic fertilizers had little or no effect. Pearsall's (1932) hypothesis that growth of blue-green algae is at least partially dependent on high organic content of the water is now rather widely accepted. The presence of amino acids in lake waters and the recent work of Hutchinson (1943) and Hutchinson & Setlow (1946) on thiamin, niacin, and biotin are most interesting.

9. The surface waters of the great majority of lakes and streams lie in the pH range of 6.0 to 8.5. *Per se*, however, the hydrogen ion concentration is believed to be of little significance. Fundamentally, pH is simply a convenient measure of the sum of a good many chemical complexities, and it is the individual members of the complex which presumably affect and limit the plankton rather than the total.

10. The dissolved oxygen content is never a limiting factor in unpolluted streams, and in lakes it seems to be important only in the hypolimnion where a concentration of about 0.2 cc. per liter is thought to be the critical point for most plankton Entomostraca and rotifers. Nevertheless, there are many records of zooplankters being taken from bottom waters with even lower concentrations during summer and winter periods of stagnation. Other dissolved gases in the hypolimnion may be limiting factors. Exceptionally high concentrations of hydrogen sulphide and carbon dioxide drive zooplankters out of the bottom waters, but it is difficult to separate the effects of these factors from oxygen lack and other associated and unusual chemical conditions.

#### PHYSICAL FACTORS

1. It almost goes without saying that a good many morphological features of lakes, as well as climatic conditions, indirectly influence the plankton. Thus, the size of the drainage area and the chemistry of the surrounding soils and rocks determine the quantities of nutrients in the water. Seepage lakes (without regular inlets and outlets) generally have smaller plankton populations than drainage lakes. Large size, regular shape, great depth, high elevation, and high latitude are all factors which tend to discourage the development of large plankton populations. As Rawson (1939) has so

appropriately put it: "while the edaphic factors determine the kinds and amounts of primary nutritive materials, the morphology of the basin and climate may to a large extent determine the utilization of these materials."

2. Qualitatively, there are no basic differences between the true plankton of running and standing waters, the same taxonomic groups being present in each. From a quantitative standpoint, however, one of the greatest detriments to the development of a plankton population is a strong current. Rapid streams in hilly or mountainous country have an almost nonexistent plankton, most of the organisms in the water being bottom forms which have been torn loose. River conditions, as contrasted with stream conditions, are much more favorable, and large, slow rivers have plankton populations which compare quantitatively with those of typical lakes. This has been demonstrated by the extensive investigations on the Illinois, San Joaquin, and upper Mississippi rivers (Kofoid 1908, Allen 1920, Galtsoff 1924, Reinhard 1931). Both phytoplankton and zooplankton are most abundant during periods of slow current and low water, while rising water levels generally produce sharp declines in the plankton as barren storm waters mix and replace the water of the channel and backwaters. Schröder (1897) has suggested a "law" to the effect that the volume of plankton in running waters is inversely proportional to the speed of the current. Although this concept is probably true in a general way, it is highly desirable that much more evidence be accumulated. When a stream is dammed, the current effect is eliminated, and the plankton rapidly becomes much more abundant and quantitatively lake-like. Conversely, if a lake has a rapid-water outlet, the typical abundant lake plankton decreases progressively downstream, being strained out by vegetation and debris of the substrate, and destroyed by the turbulence of the water and its suspended silt and sand (Chandler 1937, Reif 1939). In addition to this grinding action, high turbidity of rivers and streams, especially at times of high water, may decrease plankton populations by "silting out" the organisms and greatly decrease photosynthesis by cutting down on light penetration.

3. Although lake waters rarely are turbid in the sense that river waters are turbid, the thickness of the productive photosynthetic zone at the surface of a lake depends very largely on the amount of suspended debris and plankton, as well as on the color of the water itself. The compensation point in a lake is that depth at which photosynthesis and algal respiration exactly balance each other during a 24-hour period. In a highly colored lake with a large plankton and much suspended detritus this point may be only a meter or two below the surface. In clear lakes with little plankton it may be as deep as ten meters. Thus the fraction of the volume of a lake in which primary production goes on may be large or small.

4. In accordance with van't Hoff's law, plankton populations are undoubtedly determined to a large extent by the temperature characteristics of lakes and streams, which, in turn, are primarily dependent upon depth, wind, and insolation. Algae and zooplankton are seldom abundant during December, January, and February, and real algal "blooms" usually occur during the warmest weeks. From the standpoint of the photosynthetic process, however, it is interesting to note that the compensation point is deeper at lower water temperatures than at higher water temperatures. The low plankton production of high altitude lakes is a controversial matter; some investigators believe that it is due to low temperatures, while others maintain that it is due to inadequate dissolved nutrients. Needless to say, there is great need for fundamental research on the effects of temperature on the physiological activities of individual plankton species, including rates of feeding, reproduction and development, and length of life.

#### BIOLOGICAL FACTORS

As is true in so many other types of ecological research, some of our most fundamental difficulties in the study of plankton dynamics center around our ignorance of the biotic interrelationships of the various major and minor taxonomic categories. For example, very little information is available concerning the relative importance of living algae in the diet of zooplankters under natural conditions. Most writers have assumed that algal cells form a large and necessary part of their diet. Others, however, such as Huff (1923), present evidence to show that plankton Entomostraca are more or less independent

of living algae and may subsist almost entirely on detritus and bacteria. Certainly those of us who have mass-cultured *Daphnia* and copepods in the laboratory in soybean meal and hay infusions are well aware of the fact that algae are by no means essential for successful long-time cultures.

Although many reference works contain the guarded inference that there is a tendency toward a balance being struck between feeders and food under natural conditions, it yet remains to be conclusively demonstrated that the grazing of the zooplankton in fresh waters has an important effect on the control of phytoplankton populations. Pennington (1941) and a few other investigators have worked with zooplankton-phytoplankton ratios in the laboratory and have demonstrated in a few instances that there is a real relationship. It should be emphasized, however, that most of this experimental work has been done with relatively pure cultures, consisting of a single species of zooplankton and a single species of alga, and that both species were utilized in concentrations vastly exceeding those occurring in normal plankton communities. The fact that oxygen nearly disappeared from Pennington's cultures is indicative of abnormal conditions.

The scatter diagrams in Figure 7 may have a bearing on this problem. They show the relationship between numbers of Copepoda and Cladocera per liter and total numbers of algal cells per liter for all times of the year in seven northern Colorado lakes. All of these data emphasize the same facts; that is, a relatively low to medium phytoplankton population (less than 5,000,000 cells per liter) may support populations of grazers which range from

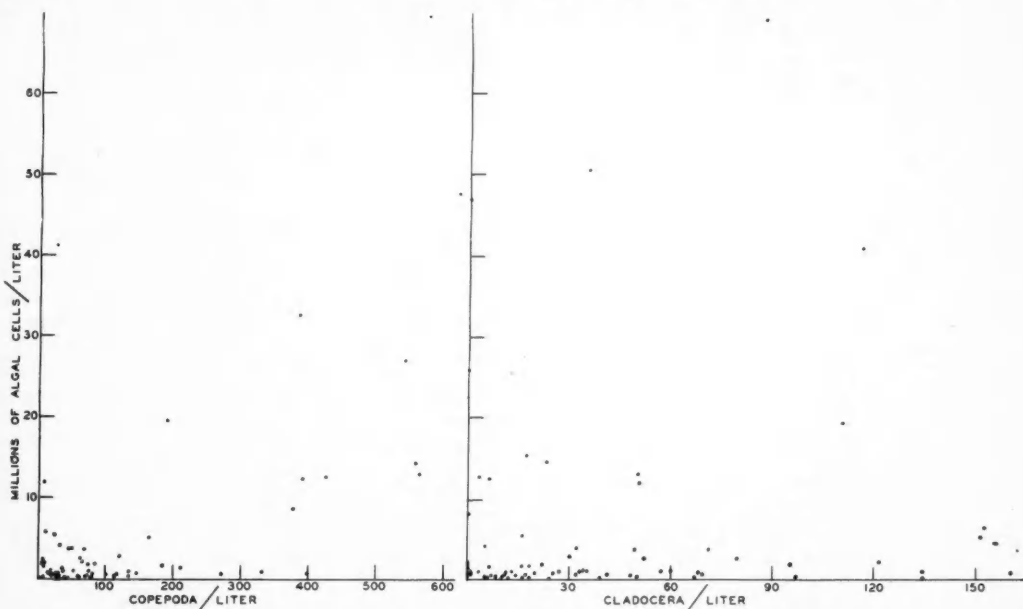


FIG. 7. Relationships between total algae and Copepoda and Cladocera in seven northern Colorado lakes. Each point represents an average population for several depths between surface and bottom on a particular day.

very low to very dense, and that dense phytoplankton populations are not necessarily associated with dense populations of grazers. The simple coefficient of correlation ( $r$ ) between Cladocera and number of algal cells per liter, for example, is only .19. The rotifer-phytoplankton data in our possession show the same general relationships, with a coefficient of .20.

These momentary numerical relationships are probably less important than the relative temporal development of zooplankton and phytoplankton pulses. Theoretically, zooplankton pulses should follow or be delayed beyond the peaks of algal pulses. This is due to the fact that algal cells divide comparatively rapidly and produce a peak before their effect as a richer food source is reflected in the more slowly reproducing rotifers and Entomostraca. But as the grazing population grows more dense, it begins to thin out the algae more rapidly than the algae can reproduce, and consequently the algae become less abundant. This is followed by an expected decrease in the grazer population due to insufficient food.

If the curves representing abundance of algae in Figure 4 are carefully compared with the grazer curves of Figures 5 and 6, however, it will be seen that this "delayed" relationship is apparent in only a few cases. The rotifer population in Gaynor Lake (Fig. 5), for example, is the reverse of total algae from May through November, with pronounced algal and rotifer pulses following each other in a striking manner and giving the general impression just outlined. There is a slight suggestion of a similar relationship for Boulder Lake. If the curves of Figures 4 and 6 are compared, it will be seen that there are no correlations, with the possible exception of a slight one between the algae and Cladocera of Boulder Lake. Data for Copepoda-phytoplankton relationships in possession of the writer are completely irregular.

Aside from comparing the relative course of phytoplankton and zooplankton pulses by inspection of these curves, however, the presence or absence of time lags in the development of zooplankton pulses after the occurrence of phytoplankton pulses may be determined by calculating the simple coefficient of correlation between phytoplankton populations on particular dates with zooplankton populations at later dates. If, for example, these calculations are made for phytoplankton populations on regular sampling dates and the corresponding Cladocera populations taken arbitrarily two weeks later (interpolated from the curves), the simple coefficient of correlation for the seven northern Colorado lakes (76 pairs of samples) is found to be only .13. A comparable calculation for phytoplankton and delayed rotifer populations is .43, a value which is significant. If, however, the highly variable data for Gaynor are not included, the coefficient of correlation between phytoplankton and delayed rotifer populations for the remaining six lakes becomes -.05. For Gaynor Lake alone (11 pairs of samples) it is .30, a value which has no significance.

Thus, from the standpoint of these seven Colorado lakes, we may conclude that (1) there are seldom obvious numerical relationships between pulses of zooplankton and algae and that these may well be fortuitous relationships, (2) food materials do not appear to be a limiting factor for the total zooplankton populations, and (3) the relative significance of algae and particulate detritus is unknown, but it is likely that the latter may be an important food source. The work of Riley (1940) on Linsley Pond is in agreement with these comments; he says, "Variations in the amount of animals do not have a significant effect on gross production or the size of the standing crop of plants."

Other biotic interrelationships are equally obscure. We know almost nothing about the food requirements or special food habits of individual zooplankters. We know little about the reproductive rates of zooplankters and phytoplankters under varying natural conditions. We know essentially nothing about intraspecific and interspecific competition for food and dissolved nutrients, nothing about optimum population densities and the antagonism of one species for another.

To all of these gaps in our knowledge of the dynamics of fresh-water plankton populations there is only one general answer and common denominator; that is, a careful study, however tedious, of individual plankton species with reference to the many varying ecological factors to which they are subjected.

#### MEASUREMENT OF PLANKTON PRODUCTION

Because of the many difficulties involved in carrying on limnological field work in cold and inclement weather, the great majority of plankton papers are concerned only with warm season conditions, few of them beginning as early as April or extending beyond September. As a result, most estimates of plankton production, no matter what the method, take little or no account of conditions during more than half of the calendar year. It is the vigorous contention of the present writer that any reasonably accurate, over all, quantitative calculation of plankton production must be based on year-round (or several years) sampling at representative depths. In other words, production should be thought of in annual, not seasonal, terms.

Production in a field of corn begins at a definite time in the spring and ceases at a definite time toward the end of the growing season, and we can therefore easily determine the total crop and the rate of production. In the plankton ecosystem, however, the whole year is the growing season, and production goes on ceaselessly at highly variable rates and with a multiple turnover and reutilization of nutrient materials. There is no time when one crop begins and ends, no time when there is any way of establishing a reasonable estimate of the total amount of plankton which has come into existence during a known interval.

Investigators in both this country and in Europe have calculated phytoplankton production for several species of algae (notably *Chlorella*) by suspending pure cultures in clear and blackened bottles at various depths in the upper waters and determining the dissolved oxygen changes over various intervals (usually less than 15 hours). In this way respiration, net carbohydrate production, and efficiency of production have been estimated. Unfortunately, however, such fundamental research has thus far supplied only a small fraction of the information we really need for the over-all picture. Ideally, we could arrive at an exact calculation of the gross (primary) phytoplankton production, or phytoplankton biomass, in a lake, if we knew the reproductive and respiratory rates of each of the common species of algae in a body of water at all depths and at all times of the year, as well as the efficiency of the photosynthetic process in each species! Because of the many obvious and insurmountable difficulties involved, such an exact calculation is purely hypothetical.

Using the large mass of data available for Lake Mendota, however, Juday (1940) has made two estimates for net total annual phytoplankton production, one based on a hypothetical weekly turnover in the organic matter of the mean annual standing crop of phytoplankton, the other on a biweekly turnover. The former calculation represents an energy value of 598, and the latter 299, gram calories per square centimeter of lake surface. Corresponding figures for the zooplankton are 22 and 11 gram calories.

It is true that the magnitude of the standing crop of plankton at any moment is not, in itself, a measure of the rate at which production is going on. Nevertheless, the mean annual standing crop is, in a general way, an index which reflects the sum total of ecological conditions in a lake. The weakest link in calculating backwards and arriving at total annual plankton production from the mean annual standing crop, as Juday has done, is the estimate of the rate of turnover. On the average during the year, does the turnover of the organic matter of the plankton occur every two weeks, every week, or every three days? How does the turnover vary with mean depth, with temperature, with the chemistry of the water, with the qualitative composition of the plankton? Until these and other questions are answered, the present writer feels that estimates of the total annual production, from the standpoint of regional and comparative limnology, are very rough approximations and that such data should be accepted with great caution or held in abeyance.

It is extremely difficult to separate and make gravimetric determinations of the phytoplankton as distinct from the zooplankton, and to separate each of these from particulate detritus. The Juday ten-liter plankton trap, the Clarke-Bumpus plankton sampler, and the plankton pump and net are all quantitative devices based on the principle of passing a known quantity of water through a bolting silk net. When these instruments are equipped with

coarse nets, the Entomostraca are retained, while many rotifers and most of the protozoa are lost; medium nets retain practically all of the zooplankton but also retain some algae and organic detritus; the finest nets, on the other hand, retain nearly all of the organisms but lose many unicellular algae and much detritus.

Alternative gravimetric methods involve the determination of *seston* including all suspended particulate organic materials, both organisms and detritus, by means of sedimentation, filtration, or centrifugation. As emphasized in a previous section, the larger portion of the *seston* may consist of detritus. Except when small lakes are badly silted by rains or flooded inlets, however, nearly all of the detritus in open waters originates from the plankton itself, and for practical purposes of measuring production it may be considered an integral part of the plankton. Indeed, Birge & Juday (1922) and Juday (1940, 1942) apparently include detritus in with the gravimetric determinations of the phytoplankton. Total *seston* is a valuable and reliable index of comparative plankton production, and it is strange that it has not been more widely used.

In addition to using gravimetric calculations to determine the mean annual standing crop, one may also take a direct census in terms of mean numbers of phytoplankters, protozoa, Rotatoria, Cladocera, and Copepoda per liter or per square centimeter of lake surface. This technique has the great advantage over gravimetric methods in that it eliminates the error of particulate detritus but has the great disadvantage in being exceedingly tedious. It should find application in the study of lake typology and in the determination of numerical ratios of the various taxonomic groups in the plankton.

Sampling and enumeration practices vary widely. Personally, we have much faith in the ten-liter Juday plankton trap supplied with a number 25 net for zooplankton, and the Foerst centrifuge for the phytoplankton and smaller species of zooplankton. Zooplankton results are usually expressed as "standard," linear, or volumetric "units" per liter (usually cubic millimeters), taking into consideration the size and volume of the cells of each species (spherical, ovoid, cylindrical, etc.). Our usage of cells per liter has the error of wide variations in cell size from species to species. This error is serious in comparing few samples or seasonal populations, but if results are expressed as mean annual numbers of cells per liter when comparing one lake with another, these variations are largely cancelled out.

Mean annual standing crops are expressed in a variety of ways for selected lakes and rivers in Table 1. Gaynor Lake, Colorado, at the top of the list, had what may be one of the most dense year-round lake plankton populations ever recorded (aside from lakes which develop true summer phytoplankton blooms), with a mean annual standing crop of 27,500,000 phytoplankton cells, 823 rotifers, and 653 Entomostraca per liter. Some individual samples from this lake contained in excess of 70,000,000



phytoplankton cells, 5,000 rotifers, and 1,000 Entomostraca per liter. The last figure is equivalent to one copepod or cladoceran per cubic centimeter, which is a much more dense population than can be attained in laboratory mass-cultures! At the other extreme is Kossler Lake, a northern Colorado lake in the foothills zone, with a mean annual population of only 900,000 phytoplankton cells, 20 Entomostraca, and 24 rotifers per liter. Many individual samples from this lake contained no Entomostraca or rotifers and only a few thousand diatom cells per liter.

Utilizing the data for the seven Colorado lakes, the Illinois River, and the San Joaquin River, the ratio of Entomostraca to phytoplankton cells per liter ranges from 1:1,800 for the San Joaquin River to 1:63,000 for Boulder Lake, Colorado. Kossler Lake, Colorado, has the second lowest ratio, 1:45,000. Corresponding ratios for rotifers and phytoplankton are equally divergent. The San Joaquin River has only 50 cells per rotifer, while Kossler Lake has 37,500, and Boulder Lake 35,900 cells per rotifer.

Some of these data appear to be additional evidence that zooplankters utilize large quantities of particulate detritus as food rather than algae, particularly in lakes with low phytoplankton populations (less than 1,000,000 cells per liter). In Allens Lake,

Colorado, for example, there was a mean annual standing crop of 109 Entomostraca and 185 rotifers per liter, amounting to 1 zooplankter to 2040 phytoplankton cells. A considerable fraction of these cells would be unsuitable for ingestion because of large size and the colonial habit, leaving perhaps 800 edible cells per zooplankter. Because of the random feeding and straining activities of the zooplankton, only a fraction of this number could be taken in each day. Therefore, even if the digestive tract were filled only two or three times a day, it is obvious that the bulk of this ingested material would be non-phytoplankton. Also, assuming that the phytoplankton cells divide on the average of once every week, it appears that the inroads on their numbers by zooplankters must be small in order to allow the persistence of a population of this magnitude.

As another and more striking example, the mean annual ratio of only 50 phytoplankton cells to one rotifer in the San Joaquin River represents an almost trivial food source.

Although the protozoan populations in Table 1 range from 1,135 to 767,350 individuals per liter, these figures are small compared with the corresponding phytoplankton populations, and it is likely that the protozoa represent only a minor element in Entomostraca and rotifer diets.

TABLE 1. Mean annual standing crop of plankton, expressed in a variety of ways, for representative lakes and rivers.

Lake or River	MEAN ANNUAL STANDING CROP						References
	Millions of algal cells per liter	Entomostraca per liter	Rotatoria per liter	Protozoa per liter	Seston, mg. per liter, ash free dry weight	Seston, kg. per hectare, ash free dry weight	
Gaynor L., Colo.....	27.5	653	823	767,350	10.91	201.7	Pennak
Boulder L., Colo.....	7.5	119	209	61,695	3.73	137.2	
Beasley Res., Colo....	2.0	225	328	15,870	1.88	31.0	
Allens L., Colo.....	0.6	109	185	88,380	1.53	99.6	
Hayden's L., Colo....	0.6	94	153	46,220	1.42	51.7	
Baseline Res., Colo....	0.9	102	467	15,740	1.39	57.7	
Kossler L., Colo.....	0.9	20	24	1,135	0.95	34.8	
San Joaquin R., Calif.	0.04	22	883	3,494			Allen (1920)
Illinois R., Ill.....	0.5	47	592	111,713			Kofoed (1908)
western Lake Erie...		23	14				Chandler (1940)
southwestern Lake Michigan...	0.9						Damman (1945)
Bridgeport L., Tex....					4.60	276.2	Harris and Silvey (1940)
Eagle Mountain L., Texas.....					2.93	134.9	
Lake Worth, Tex.....					3.80	132.9	
Lake Dallas, Tex.....					5.02	180.2	
Linsley Pond., Conn..					1.94	129.6	Riley (1940)
Quonnapaug L., Conn.					1.12	57.4	
Quassapaug L., Conn.					1.31	113.4	
Lake Monona, Wis....					3.16	267.0	Birge and Juday (1922)
Lake Mendota, Wis....					1.97	240.0	
Chautauqua L., N. Y.					1.73	122.5	Tressler, Wagner, and Bere (1940)



From the standpoint of lake volume the mean annual seston for 17 widely differing lakes ranged from 0.95 to 10.91 milligrams per liter, ash free dry weight. To our knowledge, the latter figure for Gaynor Lake, Colorado, is the highest value which has been reported in the literature. At the other extreme, incomplete data in possession of the writer indicate a mean annual seston of less than 0.40 milligrams per liter for some Colorado mountain lakes.

As shown for the seven Colorado lakes in Table 1, there is a definite relationship between phytoplankton counts and total seston only for the most productive lakes, those having less than 1,000,000 algal cells per liter showing an irregular seston-phytoplankton relationship. Except for rough correlations in lakes at either end of the production range, there seems to be little relation between zooplankton abundance and seston. This is to be expected, however, since the weight of the zooplankton is small compared with the weight of detritus and phytoplankton.

Total seston expressed in kilograms per hectare gives results which are quite different from seston expressed in milligrams per liter, because of the depth consideration in the former. For example, although Gaynor Lake had by far the greatest seston per liter, there are three lakes which exceeded it in terms of kilograms of seston per hectare. Unquestionably both of these modes of expression have a most important place in plankton production calculations. Needless to say, there is great need of much more data of the type presented in Table 1.

In addition to the methods and criteria for plankton production outlined above, there are several other indirect measurements which have been used as indexes. One such index which has been widely used during the past ten years is the colorimetric determination of the total chlorophyll content of lake waters. This quantitative method has been assumed to be a logical index, since it should give results which are proportional to the amount of energy utilized in the lake and the amount of primary organic matter formed. As emphasized by Manning and Juday (1941), however, there are many inaccuracies and objections to using this method, and it is probably useful only to a limited extent in measuring production in the epilimnion.

Other methods with limited applications include the calculation of rate of development of the absolute oxygen deficit per square centimeter of the upper limit of the hypolimnion, and the rate of plant nutrient consumption. With reference to the latter method, the work of Mead *et al.* (1943, 1945) presents interesting possibilities concerning nitrogen and phosphorus utilization data as indicators of production.

#### SUMMARY

The general composition and nutritional interrelationships of the fresh-water plankton ecosystem are discussed, with particular emphasis on the funda-

mental significance of bacteria as chemical transformers in the system.

Although a bimodal total annual plankton curve, with spring and autumn pulses, is characteristic of some lakes of medium to large area and depth, conditions in smaller and shallower lakes may be highly variable. Year-round studies on seven northern Colorado lakes showed no pulses, or one, two, or three pulses at various other times of the year. Seasonal abundance of the major taxonomic groups of algae, Cladocera, and Copepoda also varied widely from the generally accepted concepts of their definite seasonal occurrence.

Recent trends in the study of environmental factors influencing the quantitative and qualitative composition of the plankton are based on the interaction of many factors, some of which are difficult to measure. The significance of nutrients as limiting factors, ratios of ions, "trace" elements, and the probable biochemical significance of some of the many dissolved organic compounds are emphasized.

The major portion of the food of zooplankters commonly appears to consist of detritus, rather than living algae. There is very little evidence that the grazing of zooplankton has an important effect on the control of phytoplankton populations under natural conditions, and there are seldom any numerical relationships between pulses of zooplankton and phytoplankton.

Much fundamental research remains to be done on food requirements and special food habits of zooplankters, reproductive rates of all groups of plankters under varying environmental conditions, intra- and interspecific competition, and optimum densities.

Truly representative measurements of plankton production should be based on a consideration of year-round, rather than seasonal, conditions. Nevertheless, because of the many gaps in our knowledge of the activities of the plankton and the influence of environmental factors, the calculation of rate of production throughout the year can be only a very rough approximation.

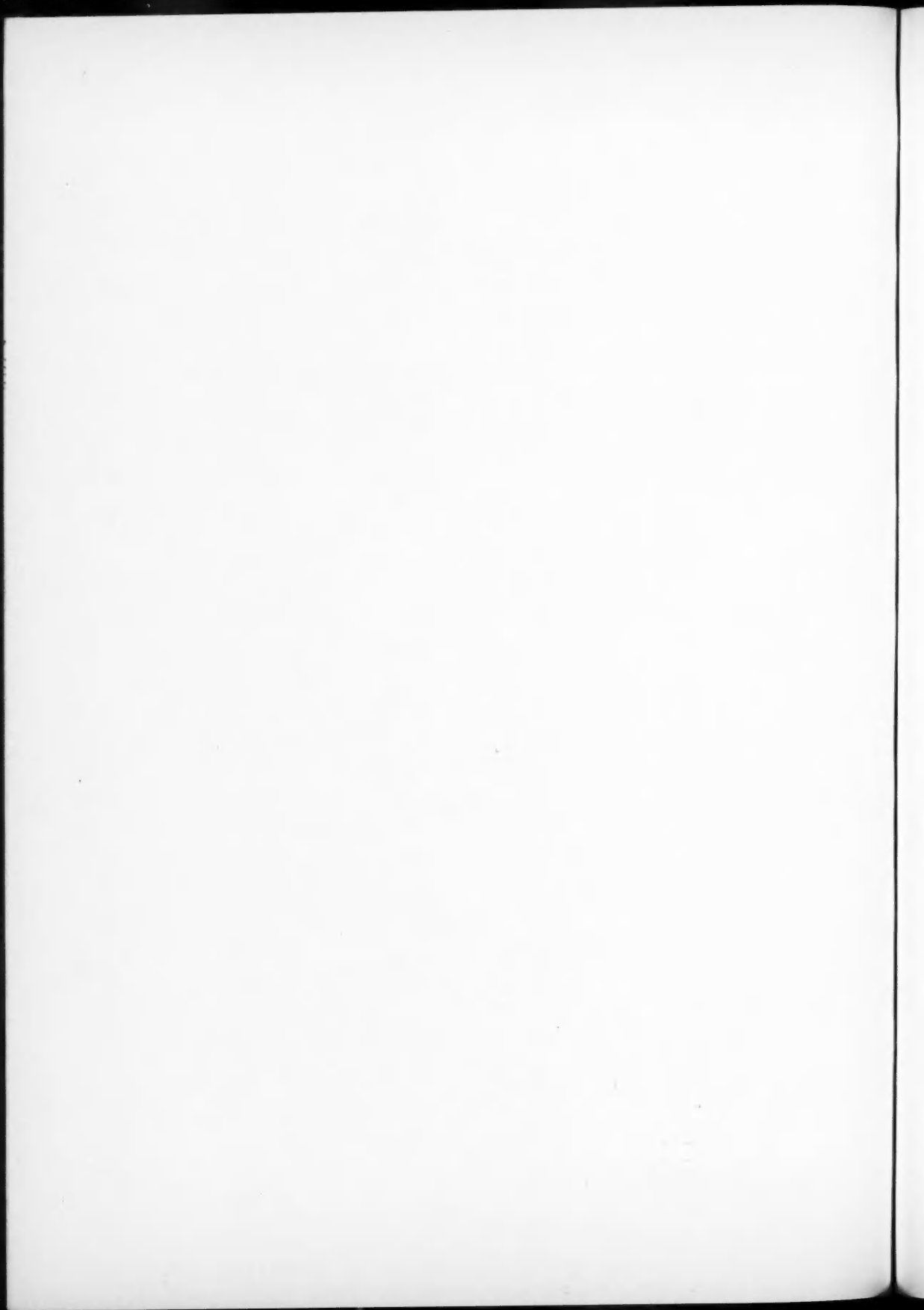
The mean annual standing crop is a general index which reflects the sum total of ecological conditions in a lake. It may be expressed in a variety of ways, including total seston per liter or hectare of lake surface, number of algae per liter, and zooplankters per liter. Total seston is probably the most satisfactory and significant means of expression for purposes of comparative limnology. When more details of the dynamics of the plankton ecosystem have been established, it should be possible to utilize mean annual standing crop data for the calculation of rate of production at the various trophic levels with reasonable accuracy.

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FACTORS IN THE DYNAMICS OF ROTIFER POPULATIONS

W. T. EDMONDSON

*Biological Laboratories, Harvard University*



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## FACTORS IN THE DYNAMICS OF ROTIFER POPULATIONS

### INTRODUCTION

The purpose of this paper is to summarize work on Rotatoria relevant to studies of aquatic production and to point out some of the most profitable lines of future investigation. The rotifers are particularly suited to studies of the intermediate levels of production. They form a very prominent part of the zooplankton of many lakes and ponds for much of the year, and by sheer numbers force themselves to attention. They are equally or even more prominent in littoral communities. As a result of the great variation in size and food habits among the species, rotifers perform a variety of functions in the aquatic food cycle. Some feed only on algae, others are carnivorous, while others are scavengers, cleaning the meat out of dead insect larvae and crustacea. Most species appear to be omnivorous, eating any particles of the right size. Thus detritus of various sorts is doubtless eaten in large quantities. Rotifers themselves are eaten by copepods and other larger organisms, and thus are presumably made available to fish. When abundant, rotifers may then play a large part in the circulation of matter through the nutrient chain. Moreover, many species are easily cultivated in the laboratory, and are good subjects for physiological experiments aimed to elucidate the structure of ecological systems and phenomena observed in natural populations.

No attempt will be made here to cover all aspects of production; rather, attention is focussed on a number of specific problems with emphasis on the rates of activities of populations and the factors controlling them. Consideration of these problems is preceded by a discussion of the occurrence of species and the limits of population size.

### FACTORS AFFECTING THE OCCURRENCE OF SPECIES

The distribution of rotifers is in general world wide. There are few abundant species which are limited to a small region of the earth. The fauna of any locality seems to depend more on the chemical and physical conditions therein than on geographically limited distribution of species. One source of information about factors which may be expected to influence production of any species is in studies which correlate distribution or occurrence with characteristics of the environment. The hydrogen ion has long been considered the most important single variable in limiting the occurrence of species. Recent work, however, seems to show that, for sessile species at least, the concentration of bicarbonate and possibly other ions may be more important. Unpublished work of Mr. F. J. Myers and the writer shows

that the hydrogen ion itself may not be effective in keeping "alkaline water" species out of acid water, but rather the lack of dissolved minerals in most acid waters. It is difficult to decide which, if any, of many substances is the most important in limiting the distribution of any species since many factors which seem to have an influence are correlated with each other. Thus, hard waters usually have a high pH. Nevertheless, pH is often a convenient and accurate index of the type of fauna which may be expected in any locality, and doubtless the hydrogen ion has distinct influences by its own physiological actions.

It is of course likely that the action of any one environmental factor is modified by variations in another, making it useless to seek any one factor as being most important. This would explain why the same species behave so differently in different locations and have different seasonal distributions. There is some evidence for this view. Remane (1929) points out that species which tolerate large differences in salinity may inhabit different biotopes in fresh and in salt water. For instance, *Notholca acuminata* is a cold stenotherm in freshwater, but in brackish water it occurs in summer at high temperatures (Carlin 1943). This and similar interactions should be studied extensively in the laboratory.

In addition to these chemical characteristics of the environment other, less definitely characterized, influences seem to have a profound effect. In general, plants with finely divided leaves have a sessile rotifer fauna richer both in number of individuals and of species than plants with flat leaves. This holds true for some other groups of animals but not all (Kreeker 1939). *Utricularia*, a plant with divided leaves, bears the richest fauna of any of the plants yet investigated, but there is as yet no explanation for the fact that it is better than the similarly shaped *Myriophyllum tenellum*.

Sometimes a species may react to two correlated factors in opposite manner. A curious example of such a conflict is furnished by *Collotheca algicola* and *Ptygura melicerta*, species which live almost exclusively in colonies of the blue green alga *Gloeotrichia* (Edmondson 1944). In addition to the type of *P. melicerta*, there are two morphological varieties, *mucicola* and *socialis*, which differ from the type also in the apparent degree of tolerance to bicarbonate concentration. The alga itself is found only in hard waters with much bicarbonate. The tolerance of the rotifers to bicarbonate is expressed as the percentage of lakes containing the forms which had bicarbonate concentrations higher than the median concentration of all lakes investigated. The tolerance may be compared with the frequency of

occurrence as expressed by the percentage of lakes containing the forms of all investigated as follows:

	Frequency of occurrence	Tolerance to bicarbonate
<i>Ptygura melicerta</i> (type).....	15	50
<i>socialis</i> .....	20	68
<i>mucicola</i> .....	40	76
<i>Collotheca algicola</i> .....	17	69

This table shows quite plainly that the greater the tolerance to bicarbonate, the greater was the number of lakes which could be inhabited. The rarity of the type form of *P. melicerta* may therefore be explained as a result of the relative scarcity of Gloeotrichia in the softer waters to which the animal is restricted, while *P. m. mucicola* is common because it can better tolerate the chemical conditions necessary for the required substrate.

The significance to production biology of such data lies in problems in which the composition of the fauna is of importance. A given species may be able to maintain itself in small numbers under sub-optimal conditions and if conditions are drastically altered, may become suddenly an important element in the fauna.

#### LIMITS OF POPULATION DEVELOPMENT

The maximum density which a rotifer population can attain is restricted by a number of factors. Presumably there is an optimal density above which the harmful effects of crowding become evident, but this has not yet been demonstrated for any rotifers. One of the basic, more general factors seems to be the amount of solid surface in unit volume of water. It has been pointed out briefly on the basis of available data that populations of plankton rotifers in lakes do not become as large as those in the littoral zone (Edmondson 1944). Thus plankton of deep lakes rarely contains more than 1000 individuals of all species per liter. The largest number found in a small weedy pond by Ahlstrom (1933) was about 5000 per liter of water. A population of sessile rotifers, chiefly of one species, has approximately 25000 individuals per liter of water in a restricted region closely associated with the substrate. The largest population of rotifers ever recorded was in the interstitial water of the damp sand at the edge of a lake, in a concentration in a limited zone equivalent to about 1,155,000 individuals of all species per liter of sample, including sand (Pennak 1940). Since the size of psammobiotic species tends to be smaller than that of littoral species, the biomasses were not necessarily in the same proportions as the numbers of individuals. It does not appear a priori that damp sand should be an optimal environment for rotifers, and in fact, the available data suggest that the average population density is greatest in the littoral region of lakes or in ponds even though enormous populations may develop momentarily in any sort of location.

Thus there is a tendency for large populations to be associated in a general way with surfaces. The

most obvious manner in which the surface operates is to provide space for sessile and thigmotropic species which do not occur in the plankton. But the situation is really more complex than this, since the surface also provides for attachment by bacteria and algae which serve as food for rotifers. Little is known of the physiology of periphytic bacteria, but it is likely that they speed the regeneration of nutrient substances in the littoral zone, thereby increasing the rate at which algae can grow. This relatively large food production can then support a larger population of rotifers and other grazing organisms.

Another possible mode of operation is that the complicated surface configuration of plants may provide nooks and crannies which act as refuges for small organisms, thus reducing the rate of loss by predation for some species. This would permit larger numbers of some elements of the population, but obviously would not explain the generally greater numbers of all kinds of organisms. Gause's experiments (1934) with *Didinium* feeding on *Paramecium* in very simplified laboratory conditions shows that a morphologically simple environment is a very dangerous place for prey in the presence of efficient predators, even in low concentration.

The general function of plants in production has received considerable attention (Klugh 1926, Kreeker 1939, Frohne 1938, Hess & Hall 1943), and the ideas briefly outlined above are generally applicable to many sorts of organisms. The importance of solid surface even to non-sessile organisms was shown by Picken (1937) in studies of protozoan communities associated with algae.

Study of the development of populations on artificial substrates introduced into the water furnishes information of interest in the present connection. Many such experiments have been made, but few investigators have dealt with rotifers. Ivlev (1933) studied the attachment of all organisms on glass slides hung in the Moscow river. A very dense population of bacteria (not enumerated), diatoms, other algae, protozoa and rotifers developed on the slides. It is obvious that these represent an addition to the biota which in large part would not have existed had the substrate not been introduced. At one station, the slides carried a maximum population of 410 rotifers per square decimeter, about equally divided between sessile and free species. The development of littoral vegetation during the growing season must have a similar function in providing for a larger fauna, and thus a role in the general productivity of a lake beyond the production of plant material alone. The composition of the periphyton has been studied quantitatively by Young (1941) and Duplakoff (1933), both of whom give many citations of literature.

#### PRODUCTION IN ROTIFER POPULATIONS

Leaving the more general considerations, problems more directly concerned with production may be taken up. In this paper, the chief measure of pro-

ductivity which will be used is the reproductive rate. If the sampling interval or duration of study is long compared to the duration of life of the organisms, then the net rate of production per individual is measured by the reproductive rate. In terms of mass, it is the reproductive rate times the mean mass of individuals. Allowance must be made for the fact that the mean size may vary from season to season. Unfortunately, data on the mass of rotifers are practically non-existent, and it is necessary in any present treatment to take the individual as a usable unit and assume the seasonal variation is small enough to be ignored. Lindeman (1941) gives the only treatment of the seasonal fluctuations in which it is possible to obtain any idea of the relative magnitude of the mass of rotifers as related to other organisms. It was not possible in his study to separate rotifers from other small zooplankton, and it is only at times when rotifers predominated in the plankton that his figures can be taken as representing rotifers.

On the other hand, in a more detailed study, the time interval will be short compared to the length of life, and it is necessary then to consider the growth rate of the organisms. For instance, in the populations studied by Edmondson (1945), small, young animals were being added at a rate greatly in excess of the deaths, and all were growing rapidly, so the mass of the population was increasing as a result of both processes. Such detailed studies are comparable to those of fish production, and the paper of Ricker (1947) may be cited for a number of approaches and viewpoints which have not yet been applied to rotifers or any other small organisms, but which should have a definite place in detailed work. When age classes can be determined, it is best to express production in terms of growth and mortality for each class. When age classes can not be determined, the reproductive rate must be used as a measure of the rate of addition of material, in short lived organisms at least. When the emphasis is on the general problem of aquatic productivity, and the rotifers are being treated merely as one link in the trophic chain, it is sufficient to use the reproductive rate as a measure of net production. Nevertheless, detailed work is desirable, and for truly quantitative work on trophic cycles, it would be necessary to know the mass or energy content of the rotifer tissue, the rates of respiration, growth, death and other vital processes.

#### REPRODUCTIVE RATES

There have been many laboratory studies of rotifer populations, but most of these have been concerned with conditions which influence the sexual cycle. A few investigators have given attention to fecundity, length of life and other points more directly involved in production. Table 1 gives a summary of data on several species reared in isolation culture and on one which could be studied under natural conditions. The data given are mean length of life, mean number of eggs laid during life, and the mean

reproductive rate which is the quotient of the first two. It should be noted that some species, as *Proales sordida*, have a period of senility during which no eggs are laid, and the tabulated values are therefore minimal for the particular conditions. The mean rates varied from 22%/day to 622%/day.

TABLE 1. Laboratory data on reproductive rates of rotifers. Data for amictic females only.

Species	Mean length of life, days	Mean number of eggs laid	Mean reproductive rate, %/day	Author
<i>Asplanchna intermedia</i> <sup>1</sup>	....	....	153	Tauson 1925
<i>Brachionus pala</i> .....	5.8	3.6	62	Kolisko 1938
<i>Cupelopagis vorax</i> <sup>2</sup> .....	42	9	21	Cori 1925
<i>Epiphanes brachionus</i> ...	8	4.3	54	Kolisko 1938
<i>Epiphanes senta</i> .....	7.3	45.4	622	Ferrie 1932
<i>Euchlanis dilatata</i> .....	12.8	6.4	50	Liebers 1937
<i>Euchlanis triquetra</i> .....	21	19	90	Lehmensick 1926
<i>Lecane inermis</i> .....	7.4	20.7	280	Miller 1931
<i>Lecane inermis</i> .....	7.8	14.8	190	Finesinger 1926
<i>Keratella aculeata</i> .....	22	8	40	Kolisko 1938
<i>Proales decipiens</i> .....	11.3	18.5	164	Liebers 1937
<i>Proales decipiens</i> .....	5.6	19.56	350	Noyes 1922
<i>Proales sordida</i> .....	8.0	24.3	304	Jennings & Lynch 1928
<i>Rotaria rotatoria</i> .....	35	4.3	12	Spemann 1925
<i>Floscularia conifera</i> <sup>3</sup> .....	4.6	....	150	Edmondson 1945
<i>Floscularia conifera</i> .....	3.1	....	140	Edmondson 1945

<sup>1</sup>Rate calculated from data for Tauson's series I. No measurement of length of life nor number of births.

<sup>2</sup>Data for a single specimen, viviparous species.

<sup>3</sup>Data obtained in natural populations. Mean length of life incorrect in original publication.

The most fecund species was *Epiphanes senta* (formerly *Hydatina*) which laid about six eggs per day under culture conditions. While there was an abundance of food in all the experiments, it is to be doubted that all the rates were necessarily measured under optimal conditions, and it is probable that at least the animals with the lowest recorded rates can reproduce more rapidly under other circumstances.

The sessile species *Floscularia conifera* possesses certain characteristics which can make it possible to measure with some accuracy the rates of reproduction, death and growth under natural conditions (Edmondson 1945). It is undesirable to go into details of technique here, but a brief indication of the method is necessary. The animals build around themselves cylindrical tubes made of small pellets. The pellets are composed of minute particles taken from the water and mixed with gelatinous secretion. Carmine or finely divided charcoal, when mixed with the water in a pond, is immediately incorporated into pellets which then mark the top of the tube at that moment. The population can then be collected and killed later, and the amount of growth of each individual measured. It is possible to recognize the young which settled on the plants after marking, and the older ones which died during the period. To estimate actual egg production, advantage was taken of the fact that the length of time it takes an egg to develop and hatch after being laid is considerably more than the interval between the laying of eggs.

Evidently, eggs can accumulate in the tubes until the first egg hatches, and the maximum number achieved therefore is determined by the rate of laying and the length of the embryonic period. The latter was estimated from the age at which the maximum number of eggs was achieved as measured by the size and mean growth rate. The rate of egg laying in two populations was estimated as 181 and 169%/day as a maximum. The corresponding rates of attachment were 48 and 118%/day. From these it appears that the combined rate of loss by death and emigration of larvae was 73 and 30%/day, respectively. Mortality probably accounted for most of the loss.

#### RATES OF NET INCREASE

The data so far discussed are essentially all we have on direct measurements of rates of reproduction. It is, however, possible to make minimal estimates of the reproductive rate in nature by measuring the maximal relative rate of increase in numbers of a species. This is made obvious by writing  $C = R - D$  or  $R = C + D$  where  $C$  is the relative rate of increase in numbers per animal present,  $R$  is the reproductive rate and  $D$  the death rate from all causes. In most species of rotifers which are an important element of the fauna, a very rapid increase in numbers takes place at some time during the year. It seems certain that at the moment when a population is increasing most rapidly, the death rate is at a minimum relative to the reproductive rate. Therefore, the maximum rate of increase can be taken as a measure of the reproductive rate at that time.

To apply this method of estimating reproductive rate in natural populations, use was made of five published sets of data, the most extensive of which is given by Carlin (1943) for frequent collections over a period of six years at Fiskeby, at the outlet

of Lake Glan in Sweden. Measurements were made on Carlin's graphs in the following way. For each species, the one year was selected during which the maximum rate of increase occurred as judged by the eye. A curve, smoothed if necessary, was drawn through the plotted values leading up to the maximum. The place on the curve was then found where the relative rate of increase was largest. The slope of the line was measured with a tangentmeter and expressed as increase in number of rotifers per liter per day. This figure was then divided by the number of animals per liter at the point measured. The result, multiplied by 100 gives the relative daily increase in the size of the population in percent per day. This method is necessary because only graphs were published. A logarithmic plot of the data would permit this figure to be determined more quickly. The other sources of data used are by Ahlstrom (1933), Chandler (1939), Colditz (1914) and Kreutner (1934). The rates were calculated directly from numbers read from tables or graphs, and since the sampling interval was rather long, they are based on the mean number of individuals present during the period of most rapid increase. The data by Carlin and Chandler were obtained at the outlets of lakes, and part of the variation in numbers may be caused by differences in the spatial distribution in the flowing system. Inspection of Carlin's graphs for the middle of Lake Glan itself indicates that little error is expected usually. All rates are listed in Table 2, and in Fig. 1 are compared with the group of direct measurements of reproductive rate.

The maximum rates of increase are as a group much lower than the direct determinations of reproductive rate. Of the three species common to both lists, *Keratella aculeata* and *Brachionus pala* have much higher reproductive rates, while the rates for

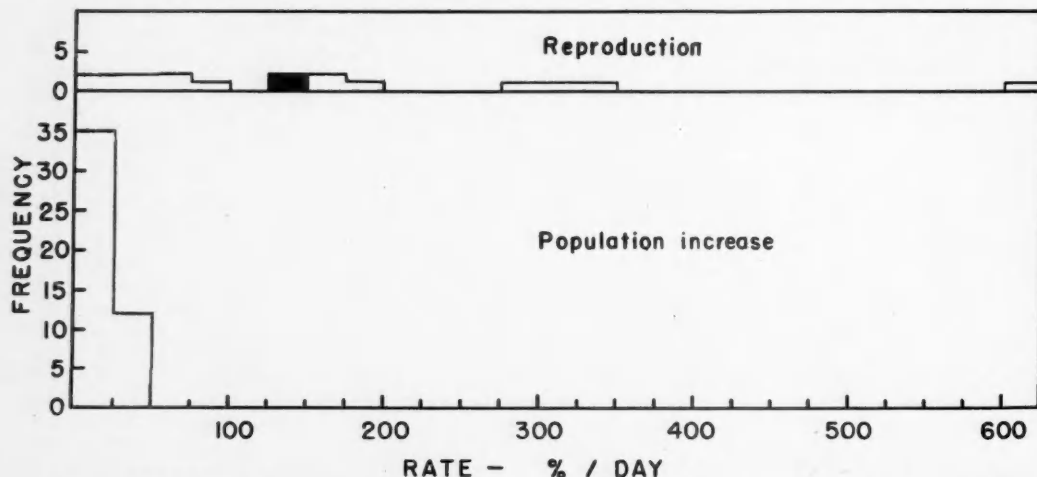


FIG. 1. Frequency distributions of measured rates of reproduction from Table 1 (above) and of maximum rate of population increase from Table 2 (below). The solid black frequencies represent natural populations of *Floscularia conifera*.



TABLE 2. Maximum relative rates of increase in number of thirty-eight species of Rotatoria observed by five investigators (%/day). The names of genera have been changed to conform with modern terminology.

Species	AUTHOR				
	Carlin	Ahlstrom	Chandler	Colditz	Kreutner
<i>Ascomorpha saltans</i> .....	15	..	..	..	..
<i>Anuracopsis fissa</i> .....	..	15	..	..	..
<i>Asplanchna brightwelli</i> .....	..	..	..	7	..
<i>Asplanchna priodonta</i> .....	7	34	..	10	15
<i>Brachionus angularis</i> .....	..	12	..	..	..
<i>Brachionus pala</i> .....	..	..	..	12	..
<i>Colurella bicuspadata</i> .....	..	20	..	..	..
<i>Conochilus unicornis</i> .....	25	11	..	..	..
<i>Euchlanis dilatata</i> .....	41	..	..	..	..
<i>Filina longicaeta</i> .....	..	18	..	..	..
<i>Filina maier</i> .....	48	..	..	7	..
<i>Filina terminalis</i> .....	..	..	..	..	15
<i>Gastropus stylifer</i> .....	38	..	26	..	..
<i>Kellicottia longispina</i> .....	16	..	13	..	..
<i>Keratella aculeata</i> .....	..	..	..	8	..
<i>Keratella cochlearis</i> .....	..	20	4	..	..
<i>Keratella hiemalis</i> .....	21	..	..	..	..
<i>Keratella stipitata</i> .....	8	..	..	..	..
<i>Keratella quadrata</i> .....	27	..	..	..	..
<i>Lecane crepidula</i> .....	..	13	..	..	..
<i>Lepadella patella</i> .....	..	19	..	..	..
<i>Monostyla closteroceera</i> .....	..	24	..	..	..
<i>Notholca caudata</i> .....	9	..	..	..	..
<i>Polarthra dolichoptera</i> .....	38	..	..	..	..
<i>Polarthra major</i> .....	31	..	..	..	..
<i>Polarthra platyptera</i> .....	..	..	..	20	10
<i>Polarthra remata</i> .....	17	..	..	..	..
<i>Polarthra trigla</i> .....	..	..	11	..	..
<i>Polarthra vulgaris</i> .....	35	..	..	..	..
<i>Pompholyx sulcata</i> .....	27	..	..	..	..
<i>Scardidium longicaudum</i> .....	..	10	..	..	..
<i>Synchaeta kitina</i> .....	17	..	..	..	..
<i>Synchaeta lakowitziana</i> .....	17	..	..	..	..
<i>Synchaeta oblonga</i> .....	20	..	..	..	..
<i>Trichocerca birostris</i> .....	17	..	..	..	..
<i>Trichocerca porcellus</i> .....	36	..	..	..	..
<i>Trichocerca pusilla</i> .....	..	30	..	..	..
<i>Trichocerca rousseleti</i> .....	19	..	..	..	..

*Euchlanis dilatata* are more nearly equal. While it may not be entirely logical to compare groups containing different species, there is no reason to expect the species which happen to have been cultured to be fundamentally more fecund than others. The impression overwhelmingly given by Fig. 2 is that in natural circumstances, populations do not increase as fast as the rotifers are capable of reproducing. This implies either that the death rate in nature is very high under the best of circumstances, or that nutritive conditions in nature are never good enough for maximal reproduction to take place. Undoubtedly both factors operate, but it seems likely that food deficiency is generally the chief cause. An examination of stomach contents and live samples should throw light on the point. Care must be taken since digestion may be very rapid (Wulfert 1939, p. 573). Dr. J. L. Brooks has found that *Daphnia* exist at suboptimal food conditions for most of the year, and reproduction is much slower than the potential rate. This work is yet to be published.

## GROWTH RATES

The pattern of growth is quite variable among the species investigated as shown in Figure 2 which compares several species by showing the length attained at various ages. *Proales decipiens* grew very rapidly during the first twelve hours of life, increasing on the average from 120 micra at hatching to 320 micra. The rate of growth was decreased when eggs were being formed within the body. *Euchlanis dilatata* grew from 160 micra at hatching to 310 micra in about one day, while *E. triquetra* did not achieve its maximal size for three or four days. The viviparous *Rotaria rotatoria* grew relatively little in length after birth, increasing on the average from 320 micra to 450 micra in about ten days. Dobers (1915) found considerable variation in the growth rate and relative increase in size among the species of bdelloid rotifers he investigated. Some sessile species apparently do not stop growing until just before death. The growth rate of *Floscularia conifera* in length appears to be somewhat higher initially than it is later in life, but during a long part of the life it is essentially constant in that the same increment of size is added each day (Edmondson 1945). Nevertheless, most of the growth takes place in the slender foot, and the rate of increase of mass probably decreases with age. The growth of most planktonic species seems to resemble that of *Euchlanis* in that most of the growth is accomplished very soon after hatching. Since most of the population is not growing, the validity of reproductive rate as a measure of production in many situations is supported.

## DEATH RATES

The most convenient way of expressing mortality is by means of the life table which gives the fraction of a uniform population alive at the beginning of successive age intervals ( $1_x$ ), the fraction dying during the interval ( $d_x$ ) and the death rate ( $q_x = d_x/1_x$ ). Data on rotifers have been summarized and references to pertinent literature have been given by Edmondson (1945). For the present purpose a brief discussion will suffice. In culture, the animals tend to have the lowest mortality when young, but the death rate suddenly increases later. This results in an  $1_x$  curve which approaches the theoretical "rectangular" type where all animals die at the same age. *Lecane inermis* has the most rectangular  $1_x$  curve yet reported for any animal. *Floscularia conifera* in natural populations is subject to causes of death in addition to "natural" mortality, and the data yield a curve more like the diagonal type. The curves are quite irregular, especially in Experiment 1. Part of the irregularity is probably caused by individual variation in growth rate which would lead to somewhat erroneous estimates of the age at death, but there is reason for believing that the populations are subject to bursts of mortality. For instance, in the experiment cited, the fraction of the initial population which died

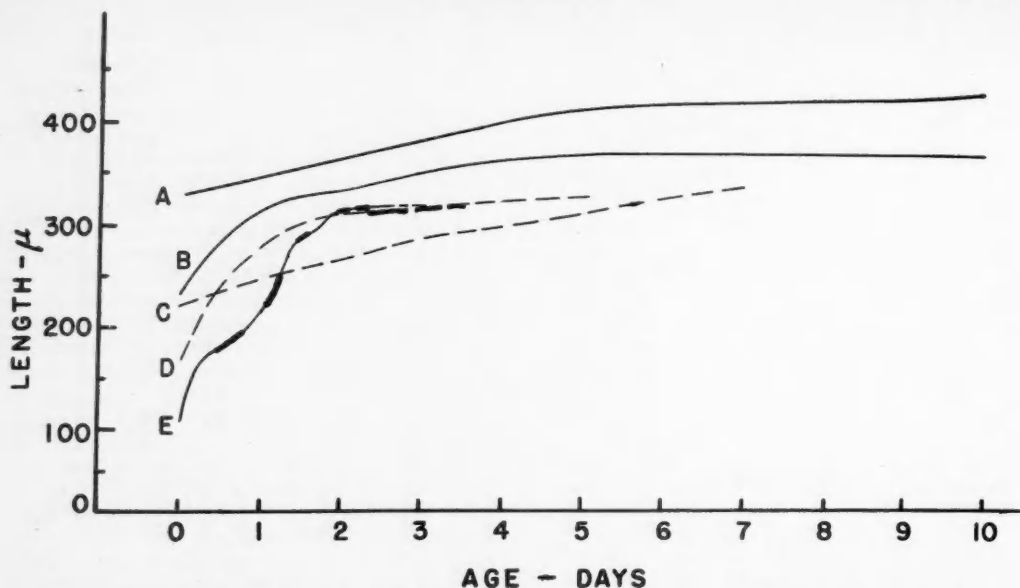


FIG. 2. Growth of several species of rotifers. The lengths attained at various ages are plotted. A. *Rotaria rotatoria* (Spemann 1924), B. *Euchlanis dilatata* (Liebers 1937), C. *Proales decipiens* (Liebers 1937), D. *Euchlanis triquetra* (Lehmensick 1926), E. *Adineta vaga* (Dobers 1915). Data from single specimens except B and E. The thickened parts of lines B and C represent times when the animals were forming eggs.

during one day was only 2%, although the mean age of the animals was 4.6 days and the mean age of those left alive was 2.6 days.

#### SEASONAL FLUCTUATIONS

The seasonal fluctuations in numbers of individuals probably represents one of the more profitable fields of investigation in connection with production. These fluctuations represent changes in the balance between increase by reproduction and loss by predation and other causes of death.

The seasonal fluctuations of total rotifer populations have been discussed by Pennak (1947). Many of the statements made there apply equally to particular species. Whenever adequate studies have been made, it has been found that there are great differences quantitatively from year to year. While all the important species may appear each year, their relative importance varies considerably. For instance, the maximum concentration achieved by *Pompholyx sulcata* in six years at the outlet of Lake Glan in Sweden was about 20, 48, 135, 240, 50 and 40 per liter in that order (Carlin 1943). Other species showed a tendency to increase steadily during the years, still others to decrease. Some varied irregularly. A number of species were remarkably constant in general seasonal distribution, although the details varied. As an example, *Asplanchna priodonta* reached a maximum in the early summer, disappeared in July, reappearing shortly in numbers of varying insignificance compared to the first maximum. The principal maximum itself varied some-

what in time of occurrence, rate of development and size. Many of Carlin's graphs are very suggestive, and the material deserves close study. Graphs for two three-year periods and a four-year period were given by Ricker (1938). These show similar irregularity from year to year and show that species do not necessarily behave in the same way in different lakes.

The present discussion will be limited to three selected species and will emphasize the rates at which populations change size. It might appear at first thought that the size of a population is the only important factor from the standpoint of predators. However, a large population maintaining itself with a low reproductive rate could very quickly be destroyed by introduction of new predators (by reproduction or migration). A similar, or even a smaller population with a greater reproductive rate could furnish more food over a longer period of time. This second population, if relieved of the pressure of predation, would naturally increase until the effects of crowding or lack of nutriment reduced reproduction. For example, of two populations of equal size reproducing two and three times a day, respectively, the second could support a rate of predation twice that supportable by the first and still maintain its size, all other things being equal. This is demonstrated by the simple equation in a previous section and by the more extended treatment by Clarke, Edmondson & Ricker (1947).

Carlin's data will be used for much of the following discussion of seasonal cycles. Of the twenty-

two species he found to be most abundant, six tolerated a large temperature range and were found throughout the year although they reached greatest abundance during the warmer months. Five species were limited to the winter, usually having their greatest abundance at less than 10°, and the other eleven were found only in the warmer months. The size of the population and rate of change was calculated from measurements made on the published graphs for four dates each month. These graphs show the measurements as well as a line fitted to ten-day means. When the line did not fit the trend of points well, as at times of exponential increase, a new line was drawn through the points.

*Euchlanis dilatata* occurred in relatively large numbers over a wide range of temperature (Fig. 3). During the course of the year, it did not appear in quantity until the temperature passed 15°; the large numbers below that temperature were waning. This fact is made clear when the relative rate of change in numbers is plotted against temperature (Fig. 4). Since the rate of change is influenced by a number of factors besides temperature, the graph is not expected to show a close correlation. There

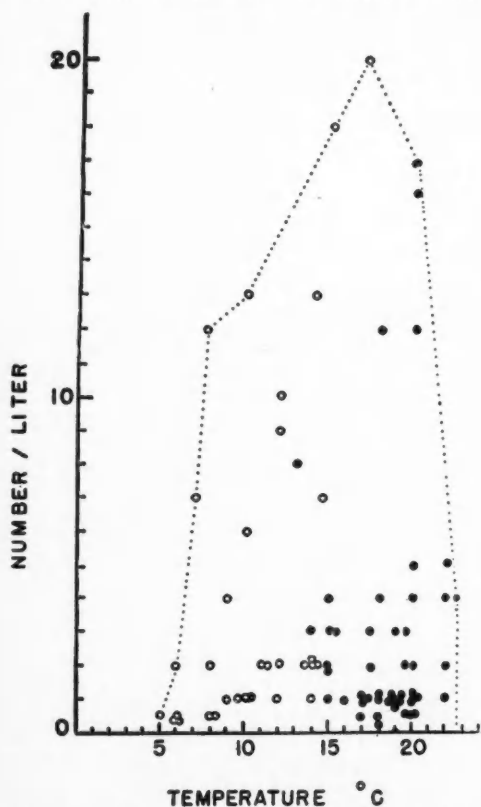


FIG. 3. Concentration of *Euchlanis dilatata* plotted against temperature. Measurements of graphs by Carlin (1943) made on four dates each month of occurrence. Open circles represent conditions after the appearance of males in the population.

are, however, several significant features. The upper limit of the field of points is sharply bounded by a straight line. It seems possible that the upper limit approximates the relationship between reproductive rate and temperature under the conditions which existed. The downward scattering of points from this line then represents the action of predation and lack of sufficient food. Some of the scatter is likely caused by error of measurement. In a more complete interpretation it would be necessary to know the rate of production of food organisms, the rate of feeding of the rotifers, and the rate of loss of rotifers. Some of the most rapid increases of *Euchlanis dilatata* took place when there was a bloom of *Oscillatoria* which is eaten freely. Some of the apparent effect of temperature may be attributable to a fair correlation between concentration of *Oscillatoria* and temperature. While laboratory work is required to establish with accuracy the relationships, this sort of situation is amenable to analysis of field data by multiple regression techniques (Riley 1939).

The open circles in the graphs represent measurements made after the appearance of males. Males usually appeared at the time of the maximum, but in one year were considerably delayed, developing when the population had fallen to a low level, and another year did not occur at all. Since fertilized eggs take a relatively long time to hatch, the appearance of males would be expected to reduce the rate of population increase even if the rate of loss to predation and the rate of laying eggs were the same as before. Factors regulating the appearance of males have not been studied experimentally in this species. In other species, temperature, nutrition, chemistry of the water or sudden changes in any of these have variously been indicated as influencing the sexual cycle. There is a large literature on this subject which is not appropriate for detailed discussion here, but reference may be made to papers by Wesenberg-Lund (1930), Shull (1929) and some of the works cited above in Table 1. The graphs for *Euchlanis dilatata* suggest that temperature is of major importance.

*Pompholyx sulcata* occurred in quantity for a short time only each year, and sizable populations were found only at high temperatures (Fig. 5). The relative rate of change, plotted against temperature, showed similarity to that of *Euchlanis dilatata* in that the upper boundary was sharply limited, but with a maximum at 19° (Fig. 6). The significance of this plot is questionable, but the points show an obvious trend. No males were ever observed, and the decline of the population cannot be attributed to the formation of fertilized resting eggs.

*Sychaeta lakowitzi* was investigated as an example of a winter species (Fig. 7). The relative rate of change in numbers, plotted against temperature, shows a less clear boundary than the previous graphs, but there is a definite tendency for the rate to rise with temperature to about 9° C. (Fig. 8), despite the fact that the largest numbers existed at lower temperatures. Males were present at almost

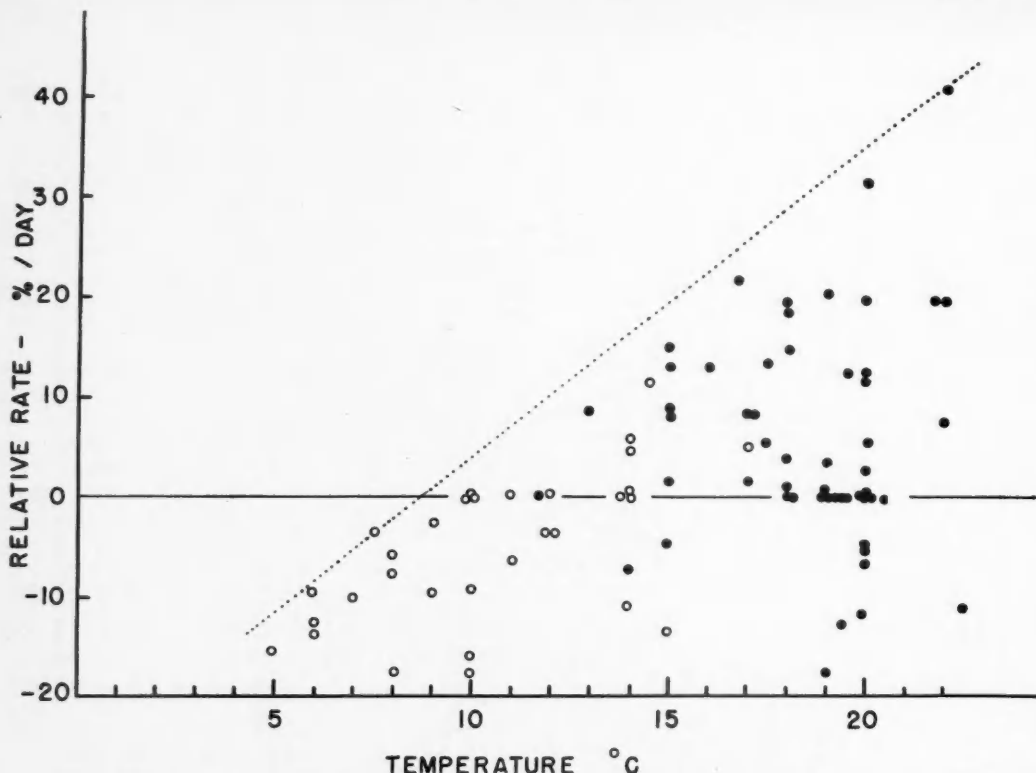


FIG. 4. Relative rate of change of concentration of *Euchlanis dilatata* plotted against temperature. Measurements of graphs by Carlin (1943) made on four dates each month of occurrence.

all high temperatures, but even so, the populations increased much of the time.

A species like *Synchaeta lakowitziana* so physiologically adapted that it can grow and reproduce at low temperatures may be at an advantage, since predation may be expected to be lower in winter than during summer. At Fiskeby, large copepods, which are known to eat rotifers (Naumann 1923), were practically absent during the winter. Cryptomonas, diatoms and blue green algae were also at a minimum, but evidently there was enough particulate organic matter present to support the flourishing population of winter species. The total rotifer population was smaller during the winter, of course. Rotifers which require large algae or other organisms are probably at a nutritional disadvantage much of the year compared to species which eat freely minute particles of detritus. These considerations lead us to examine in more detail factors which fluctuate seasonally and which seem likely, on a physiological basis, to affect the processes discussed. The most obvious factors are temperature and food. It is doubtful whether such factors as pH and dissolved substances are very important in determining large scale seasonal changes in the epilimnetic plankton of

large freshwater lakes, for these factors usually do not fluctuate more than can be tolerated by the predominant species. For instance, at Fiskeby, the pH was fairly constant during the year, rising abruptly only when there was a bloom of algae; no catastrophic effect on the rotifers is discernible in the graphs presented by Carlin. In some locations, it is quite possible that such a change could have a marked influence on the population, if it passed the limits of tolerance of many of the species present. This would be expected in the case of moderately mineralized lakes in which the pH fluctuated across neutrality. In ponds and small lakes, there are apt to be more violent fluctuations in the chemical factors, and they may be expected to have a profound influence on the populations.

#### TEMPERATURE

Temperature may be imagined as a sort of master control which determines the basic rates at which organisms can metabolize. The manner in which temperature operates is complex; by affecting the rates of biochemical processes inside the organisms variously, it affects the rates of feeding, reproduction, the length of life and rate of development of eggs. An indirect effect comes from seasonal changes

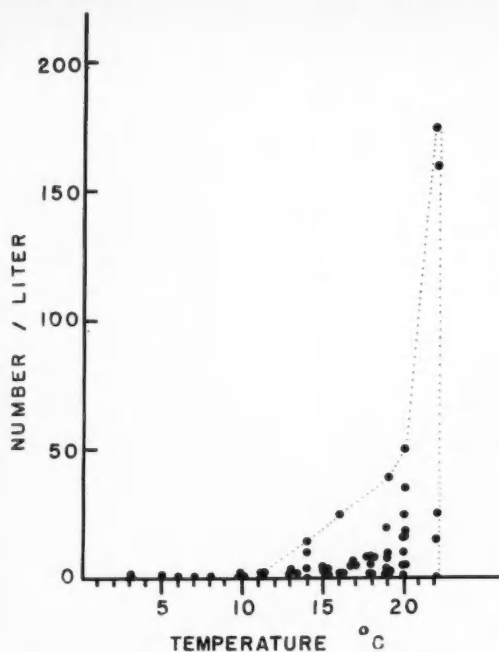


FIG. 5. Concentration of *Pompholyx sulcata* plotted against temperature. Explanation as in Fig. 3.

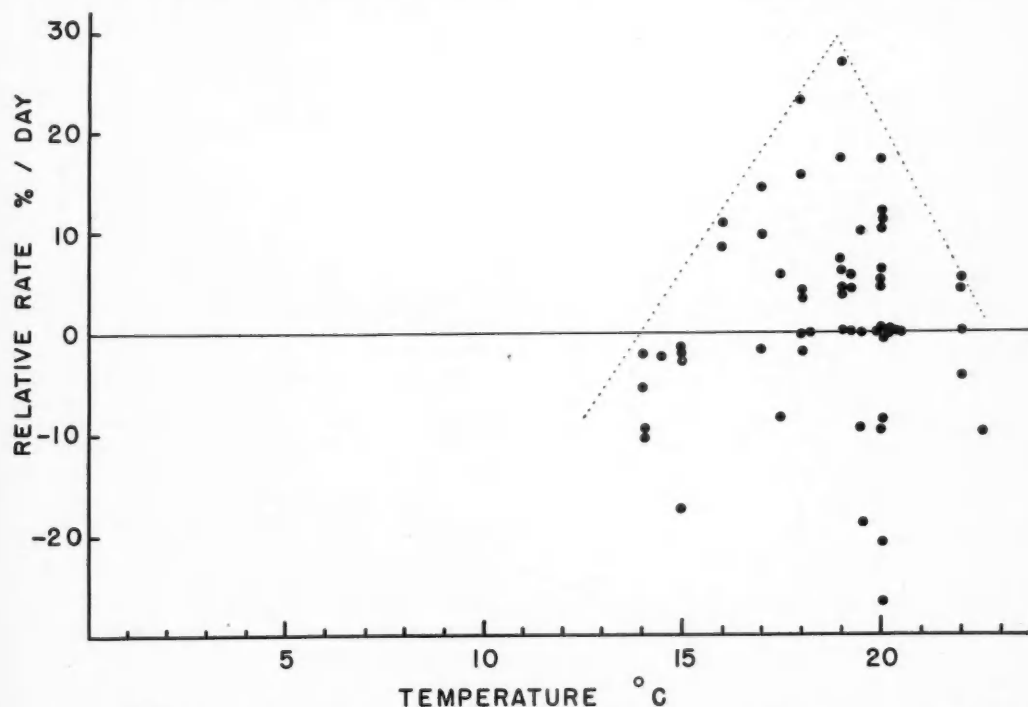


FIG. 6. Relative rate of change of concentration of *Pompholyx sulcata* plotted against temperature. Explanation as in Fig. 4.

in activities of food and predatory organisms which themselves respond to temperature.

The response to temperature by rotifers was studied by Finesinger (1926) who reared *Lecane inermis* at different temperatures with standard food concentration (Fig. 9). The length of life tended to become shorter as temperature increased, but there was an optimal range for egg production. The reproductive rate resulting was highest at 27° and 29° C. Finesinger calculated the temperature coefficient of the change of length of life by temperature, and noted that up to 29° it agreed fairly well with van't Hoff's law which calls for a change in the rate of a process by a factor of 2 for each 10° C. change.

In laboratory experiments on *Floscularia conferta* by the writer, the animals did not feed nor lay eggs at 10° C., and eggs subjected to this temperature apparently stopped developing. The animals used had been living at temperatures between 18° and 20° C. This, in common with most sessile species, is not found at low temperatures in nature. This fact may in some way be correlated with the seasonal development of substrate vegetation, but substrate cannot be held accountable for the general disappearance of many species as the temperature drops below 15°.



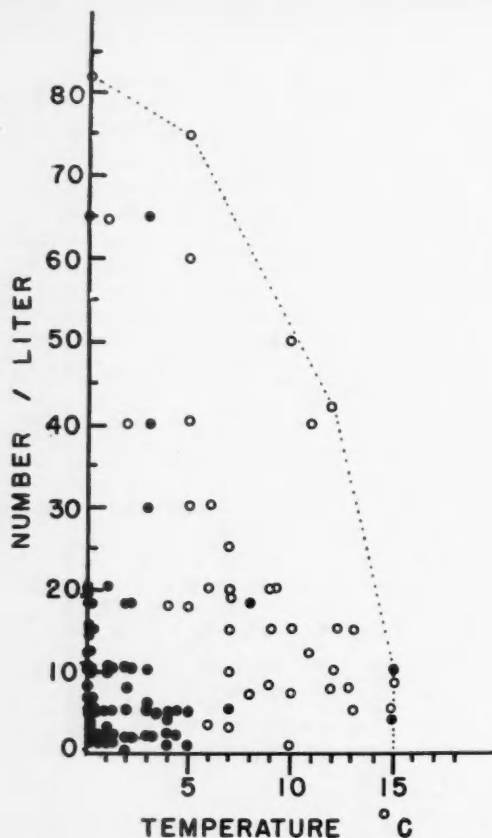


FIG. 7. Concentration of *Synchaeta lakowitziana* plotted against temperature. Explanation as in Fig. 3.

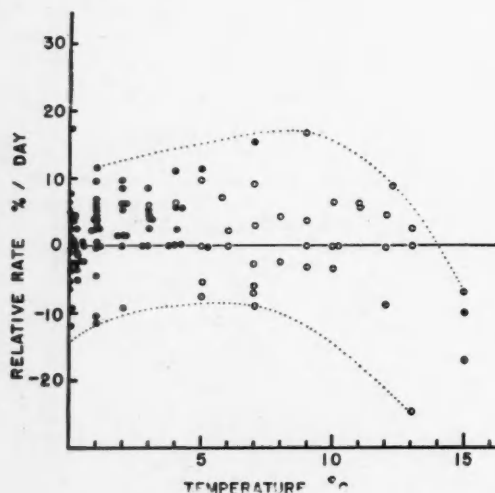


FIG. 8. Relative rate of change of concentration of *Synchaeta lakowitziana* plotted against temperature. Explanation as in Fig. 4.

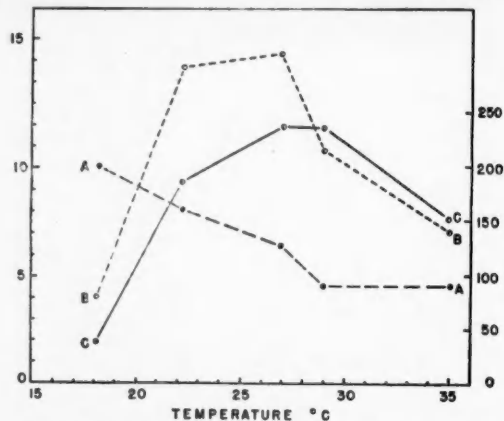


FIG. 9. Response of *Lecane inermis* to temperature. A. Mean length of life, days (left scale). B. Mean number of eggs laid during life (left scale). C. Mean reproductive rate, percent per day =  $B/A \cdot 100$  (right scale). Data from Finesinger (1926).

#### FOOD

Food is of undoubted importance to any group of consuming organisms, but there have been few special studies of food of rotifers, although many qualitative observations are scattered through the literature. There are good correlations between the structure of the trophi, kind of food and method of feeding (Gosse 1856, Remane 1929-1932). Naumann (1923) gave data on the size of particles eaten by various genera as follows: *Keratella* small algae up to 10 miera, *Kellicottia* (*Notholca*) and *Conochiloides* "very small nannoplankton," *Filinia* (*Triarthra*) nothing over 7.5 miera, *Asplanchna* all plankton larger than 15 miera.

Naumann also put rotifers in suspensions of fine carmine. These particles were swallowed by *Keratella*, *Conochiloides* and *Filinia* but not by *Asplanchna*, *Polyarthra* nor *Synchaeta*. Carlin (1943) observed that *Asplanchna priodonta* ate *Cyclotella*, that *Euchlanis dilatata* ate *Cyclotella* and blue-green algae, while *Melosira* and *Asterionella* were eaten by *Notholca caudata*. Recognizable fragments were not found in a number of species, the inference being that they do not eat diatoms. *Asplanchna priodonta* is known to eat sizable animals such as the rotifer *Keratella cochlearis* and even small *Chydorus* and *Bosmina*. Many species can pierce the walls of plant or animal plankters and pump out the contents; examples are *Synchaeta* and the larger *Trichocerca*, with virgate trophi. Many species show a certain degree of selection. Those with evertible forepate trophi catch small organisms individually, the size apparently dependent on the size of the rotifer. The remarkable behavior of *Dicranophorus thysanus* feeding on small cladocera by inserting its head between the valves of the shell is an example of very special feeding habits, although the species is able to use other food. On the whole, such specializations are rare among the rotifers, and most species

are rather omnivorous, swallowing all particles of the right size.

The effect of food concentration was studied in the laboratory by Liebers (1937) who raised small groups of *Proales decipiens* in various dilutions of a *Chlamydomonas* culture. Both the length of life and the total number of eggs laid were decreased by dilution, but the former more rapidly, with the result that the mean reproductive rate also decreased. The results are plotted in Fig. 10 where the dilution is expressed as the volume to which a certain amount of food culture was diluted. Data for the lowest dilution are based on sixteen control animals, while the others are based on six or three. Halving the concentration of food had no significant effect, but further dilution made considerable difference to reproduction. Unfortunately, there is no record of the absolute concentration of *Chlamydomonas* in these experiments, and thus no way of comparing the amount of food available with that in natural conditions. Some authors (Spemann 1924, Liebers 1937) have measured growth rate of rotifers put into filtered water. After a slight increase in size, they invariably decreased and died.

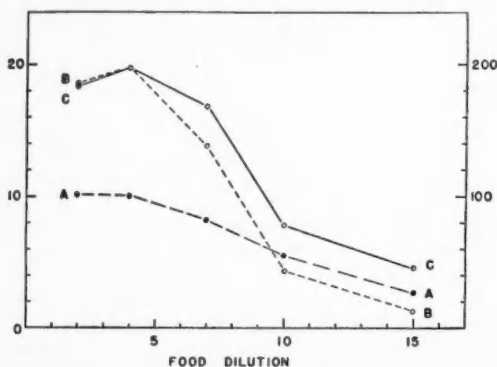


FIG. 10. Response of *Proales decipiens* to concentration of food. A. Mean length of life, days (left scale). B. Mean number of eggs laid during life (left scale). C. Mean reproductive rate, percent per day (right scale).

The effects of long continued deficient nutrition on lines of *Proales sordida* were studied by Lynch & Smith (1931). Both fecundity and length of life were depressed by lack of food, as would be expected. Both the response to dilution of food and recovery when returned to full strength culture medium were influenced by variations in temperature. The starved individuals were somewhat smaller than well fed ones, and had a different appearance. This suggests that nutritive conditions in nature may sometimes be evaluated qualitatively by examination of individuals.

The rate of feeding has never been measured directly and it is not known whether the concentration of food has any effect on the feeding activities. It is known that the rate of filtration of water by the marine copepod *Calanus finmarchicus* is not in-

fluenced by the concentration of diatoms in the water over a wide range (Fuller 1937).

The ratio of number of individuals of a species to number of food organisms at any moment depends largely on the past history of the population, and obviously shows wide variations from time to time. These variations must depend on the response of the food organisms to environmental changes, on the response of the rotifers to changes in food, on the rate of grazing, and on the availability of other food material. Without a knowledge of the reproductive rate of the food organisms and of the grazing and reproductive rate of the rotifers, it is doubtful that the significance of the ratio can be evaluated, although the direction of its change may be suggestive. It may frequently happen with many species that the supply of organic detritus is so great that the grazing on phytoplankton by omnivorous species is reduced to insignificance for a time.

A complete study of the seasonal variation requires more observations than are usually made in plankton studies. In the cases just considered, stomach analysis and observations on live plankton samples would give an idea of the proportions in which various foods were actually being eaten. Determination of predators would permit some idea of the intensity of predation. These could be better determined by well arranged experiments in the laboratory. With properly weighted figures, the changes in numbers could be expressed as functions of temperature, food and predators, and residual variations would be attributable to factors not taken into account. This is a difficult program, but it is only such studies which will show how fast rotifers (or any other consumers) are eating, reproducing and being eaten at various times, and exhibit their function in the aquatic food cycle.

#### EFFECT OF AGGREGATION ON PRODUCTION

The general biological effects of aggregation are so well known from a great number of studies that it is not necessary to discuss them here (Allee 1931, 1938). It should be pointed out that these effects can influence production in nature, as has been demonstrated in the sessile species *Floscularia conifera*. The method of determining growth and reproductive rates was described earlier in this paper. The species often forms clusters or colonies when young build their tubes on tubes of animals already present. If the solitary and colonial animals are studied separately, it is found that while both grow at the same rate after becoming established, the colonial individuals live about twice as long as the solitary ones. The rates of reproduction of solitary animals were roughly 60% and 50% of those of colonial animals in two populations. Moreover, the colonial animals started laying eggs more than half a day earlier than solitary ones.

These results are shown about as strongly by colonies of two animals as by larger colonies, and

the effect therefore is very critically dependent on the attachment of one animal to another. Whether the same effect would be shown by animals attached close together on a common substrate has not been determined. The proportion of solitary individuals in *Floecularia* populations varies greatly from time to time, and such effects may be of importance in the seasonal cycle of events. Whether similar beneficial or deleterious effects occur in natural populations of free swimming rotifers is unknown, but it is doubtful if rotifers often become crowded enough to be harmed.

#### RELATION OF ROTIFERS TO PHYTOPLANKTON

The effect of the grazing of rotifers on a rather homogeneous but dense population of phytoplankton was studied by Pennington (1942). It was noticed that experimental cultures of the small flagellate alga *Diogenes* in 100 liter outdoor tubs usually died off rapidly after achieving a very high density. Observations showed that at such times there were always great numbers of *Daphnia* or, more usually, the rotifer *Brachionus pala* present in great quantity, with their guts stuffed with the alga. Two series of experiments were then made. In the first series, three 100 cc. beakers were filled with a dense culture of *Diogenes*. To one, 1700 *Brachionus* were added, and to another 100 *Daphnia*. During the next five days the number of *Diogenes* was consistently less in the beaker with rotifers than in the control, while *Daphnia* nearly exterminated the algae from the third beaker (Fig. 11). Unfortunately, experiments with varied concentrations of rotifers and algae were not tried.

More extensive experiments were performed in the large tubs and more spectacular results achieved. The algal population was allowed to achieve a heavy density of about 10,000 per cubic millimeter, and one tub was inoculated with rotifers at an initial con-

centration of about 34,000 per liter. The population of living rotifers remained roughly at that level for about ten days during which the density of algae was reduced to a very low level. About eight days after inoculation, oxygen disappeared from the tubs and large numbers of dead *Brachionus* appeared. The numbers of living rotifers fell sharply whereupon the algae reproduced rapidly and surpassed their original concentration. Evidently there were some animals left alive, but the experiment was not continued long enough to see if the cycle would be repeated. Apparently the depletion of oxygen resulted from respiration of the rotifers and from bacterial decomposition. Pennington remarks that similar "massaeres" occur in small eutrophic ponds. It is doubtful if such effects occur in lakes or other sizable waters.

This investigation is of interest here because it permits a calculation of the rate of grazing. In the beaker experiments, the effective mean rate of reproduction of *Diogenes* as measured by the control was 1307 cells/mm<sup>3</sup>/day during the experiment, while in the beakers with *Brachionus* and *Daphnia*, the rate of change of numbers was 487 and -892 (decrease) cells/mm<sup>3</sup>/day respectively. By subtraction, it appears that the rate of grazing by *Brachionus* and *Daphnia* was 820 and 2199 *Diogenes*/mm<sup>3</sup>/day respectively. Expressed on a relative basis, the rate of increase of *Diogenes* in the control was 19%/day, and in the beaker with *Brachionus* was 8%/day. There were 17 rotifers and 1 *Daphnia* per cc., and the rates of grazing per animal were 48,200 *Diogenes*/*Brachionus*/day and 2,199,000 *Diogenes*/*Daphnia*/day. Thus one *Daphnia* ate as fast as about 45 of the rotifers. In the tub experiment, the control population was declining slowly, while that with *Brachionus* was falling rapidly. The difference in rates was 416 *Diogenes*/mm<sup>3</sup>/day, and since there were about 34 rotifers/cc., the rate was 12,200 *Diogenes*/*Brachionus*/day, about a quarter as fast as in the beaker experiments.

If these figures correctly estimate the average number of *Diogenes* eaten by *Brachionus* each day, a calculation can be made to show how the volume of *Diogenes* is related to that of the rotifer stomach. The diameter of *Diogenes* varies between 1.5 and 2.0 micra (Pennington 1941). Measurements of a figure by Hudson and Gosse (1886) suggests that the volume of the stomach of *Brachionus pala* is about 137,000 cubic micra. From these it is calculated that in the beaker and tub experiments, the rotifers filled their stomachs 1.2 and 0.3 times a day. These figures are suspiciously low, for the impression one gets from looking at rotifers is that they are constantly eating. Nevertheless, the number of algal cells consumed is enormous. While the density of rotifers was very high in the experiments, so was that of the algae, and it is proper to conclude that rotifers may have significant effects as consumers. Further experiments with varied concentrations of both organisms and with food organisms of various sizes would be illuminating, for it is not certain that

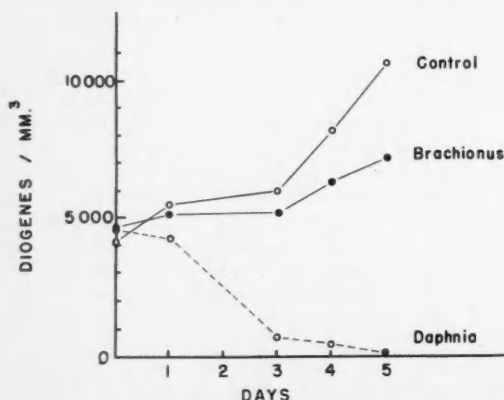


FIG. 11. Concentration of the alga *Diogenes* in three cultures on successive days. The control contained no grazing animals and represents free growth of the population. The other cultures contained 17 *Brachionus pala* and 1 *Daphnia* per cc. respectively. (Data from Pennington 1942.)

such a small alga is most efficiently eaten by *Brachionus*. It is quite possible, for instance, that in light concentration the probability of an algal cell being eaten is low enough that a stock population of algae could exist in the presence of fair numbers of rotifers and be available to repopulate the area when the rotifers decreased.

### CONCLUSIONS

From the discussion in this paper it is evident that in the rotifers, studies of production, as the word is used here, are very rare. It may be worthwhile then to point out the lines along which work is most needed and where the most profitable fields are. In addition to papers cited in the preceding text, there are only a few which deal with quantitative work on long continued collections. While these papers report fluctuations in the numbers of rotifers and other organisms, there has been little evaluation of the data in what we may call dynamic terms; that is, no study of the rates at which numbers rise and fall, and of the interrelationships with the activities of other organisms and changes in the environment. Since the density of a population at any moment is related to the rate of population change and the time over which it has operated, it seems reasonable to study the rate directly. Attention should be given to all possible ways of resolving the change in population size into rates of reproduction and death, and of relating these to the environment.

A number of sessile species can be studied by the carmine method, and possibly a modification will extend the method to many other species. Most sessile rotifers make clear gelatinous tubes which do not take up carmine, but which probably could be stained with a vital stain such as neutral red or brilliant cresyl blue. There has been no attempt to do this with a natural population. If such dyes can be used successfully, we have the possibility of making complete studies on entire populations of sessile rotifers, and indeed on other organisms as well.

Greater general interest attaches to plankton populations, but they offer much greater technical difficulties. There are a few methods which have not yet been exploited, and it may be possible to improve the approach to plankton by special observations. For example, a number of planktonic species carry eggs attached to the body before hatching, and if they accumulate in significant numbers, an approximation to the rate of laying eggs is possible by a method analogous to that used for *Floscularia conifera*. In this case, an independent measure of the rate of egg development is needed. Freshly collected eggs, reared at proper temperature may give a close enough estimate. Naturally statistical allowance would have to be made of eggs which came loose from the parent's body, but the situation is not entirely impossible. A series of such measurements together with measurements of changes in the standing crop would permit an estimate of the mean rate of loss.

Studies of this sort are of course incomplete and can not yield as much detailed information as is de-

sired. There is great need for pertinent physiological experiments in the laboratory in which the effects of variation of several factors are studied. Species should be chosen for study which can also be studied in natural populations, for the experimental work should be designed to explain natural phenomena, and observations in nature will show whether enough laboratory work has been done on a given point, and whether some important factor has been overlooked. Neither type of study is complete in itself. Unfortunately, to date no serious culture work has been achieved with truly planktonic species, and the most famous laboratory rotifer, *Epiphanes senta* (Hydatina) is not an important element in the fauna of natural waters. One of the first steps is to overcome the difficulties of cultivating planktonic species. Once the ranges of effect of important environmental factors are determined for the chief species, we will be in a much better position to evaluate data on natural populations.

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PRODUCTION AND UTILIZATION OF FISH POPULATIONS

WILLIAM E. RICKER  
*Indiana University*

CONTRIBUTION No. 355, DEPARTMENT OF ZOOLOGY, INDIANA UNIVERSITY

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## PRODUCTION AND UTILIZATION OF FISH POPULATIONS

### GENERAL OBSERVATIONS

Clarke (MS) has presented an analysis of the process of production in an ecosystem, which can serve as a theoretical basis for the study of any phase of it. The net elaboration of green plant substance is consumed by animals or used by heterotrophic plants; and these primary consumers are themselves consumed by other organisms either before or after their death. The production of a fish population is based on the processes of feeding, digestion and assimilation, and the transformation of a part of the assimilated food to new body substance. For a quantitative analysis of the process, it is convenient to distinguish the following lines of investigation:

- a. A study of the quantities of different kinds of foods available to a fish in its natural habitat.
- b. A study of the factors affecting the rate of food consumption by fishes.
- c. A study of the fraction of available natural foods which are actually utilized by the fish.
- d. A study of the fraction of the food eaten which is used for growth by the fish. This can be subdivided into (1) the percentage of assimilation of the food consumed, and (2) the percentage of the food assimilated which is used for growth; though direct determinations of the ratio of growth to consumption are more common.
- e. A study of production as determined directly from the fish population itself, on the basis of its rate of growth and rate of mortality.

In order to bring utilization or yield into the picture, we must add also:

- f. A study of what fraction of the production of a fish population is used by man, the effect of such utilization upon the population, and the means whereby total yield can be increased as far as possible, consistent with economy of effort in its capture.

Before reviewing some of the progress which has been made along these lines, we may consider briefly the kinds of foods which fishes eat. Classified on the basis of their food habits, they fall into three great divisions: plankton-eaters, bottom-feeders, and fish-eaters. Naturally there are species which occupy intermediate positions, and a majority of fishes start out in life as plankton-eaters, regardless of what their later food may become. Nevertheless these divisions are useful.

The plankton-eaters in general tend to be small in size, though they include the largest of all fishes, the basking shark. Typical consumers of plankton are such species as the herrings, menhaden and pilchards in the ocean, and the ciscoes or lake herrings in our

Great Lakes. These fish exist in tremendous numbers, and form the basis of some of our most important fisheries. For example, the catch of California sardines in the eastern Pacific ocean was in the neighborhood of 700,000 tons annually during the early 1940's, which was at least twice the weight of all other fishes landed on the west coast of this country.

The bottom-feeding fishes include such well-known food fishes as the haddock and halibut in the ocean, or the whitefish in our Great Lakes. These spend most of their time near the sea or lake floor, eating the invertebrate animals which cover it.

Finally, the fish-eating species tend to include most of our largest fishes—such species as the tuna, swordfish and spring salmon in the ocean, or the pike and lake trout in fresh waters.

### STANDING CROP AND PRODUCTION OF FISH FOODS

Almost all the macroscopic organisms in a body of water can serve as food for fishes of one sort or another, so that quantitative studies of the occurrence of any such organism are of potential value in estimating the capacity of the body of water to support life. This subject naturally is far too broad to be considered here. Descriptions of special techniques for enumerating organisms of different sorts, and the results achieved, comprise a major part of limnological and oceanographical literature. There are relatively few kinds of organisms or habitats for which a technique of quantitative study is not now available.

While investigations of the *crops* of fish food animals are numerous, accurate estimates of their *production* are very scarce. Possibly the only satisfactory attempts to draw up complete year-round balance sheets of production for invertebrate animals, without relying heavily on guesswork, are those of Borutsky (1939, 1939a) for the chironomids and other profundal bottom organisms of Lake Beloe near Moscow. Less ambitious but still factually based estimates, of summer production at least, are those of Lundbeck (1926) and Miller (1941). Every other such estimate known to the writer depends on a more or less arbitrary estimate of the rate of "turnover" of the organisms concerned (Juday 1940, Deevey 1941, Lindeman 1941).

In default of accurate information concerning their production, the standing crops of fish foods have been widely used as a relative measure of food productivity. Such a measure is certainly more useful than none at all, though naturally no exact correspondence can be anticipated. There must obviously

be some correlation between standing crop and production, *within* any assemblage of similar organisms living in similar habitats. It would be desirable nevertheless to have more information concerning the relation of the size of a crop of fish food to its production, or to the size of the crop or of the production of the fishes which feed on it. In a general way, a relationship of this sort is suggested by the fact that the shallower parts of both fresh and salt waters tend to have a richer fauna, of both invertebrates and fishes, than do the deeper parts. Within a shallow area in the vicinity of Cape Cod, Lee (1944) noted that flatfishes were commoner on bottoms having an abundance of the polychaete *Clymenella* and the amphipod *Ampelisca* which he believed (unfortunately had not observed) to be among the most readily available foods of the region. In the case of certain rather shallow Swedish lakes, Alm (1922) has found a suggestive relationship between the annual yield of fish and the summer standing crop of benthos—the F/B coefficient.

#### RATE OF FEEDING BY FISHES

The quantity of food consumed each day by a fish, expressed as a fraction or percentage of its total weight, is usually referred to as the *daily ration*. Ideally it should be expressed in terms of the calorific equivalent of both food and fish. The direct study of what influences affect the size of the daily ration has been carried out chiefly under experimental conditions. Pertinent observations under natural conditions are also available in the form of the frequency of occurrence or average amount of food in stomachs; for under certain circumstances these can be taken as a relative index of rate of consumption, thus avoiding the more difficult measurement of actual amounts ingested.

#### TEMPERATURE

There is good evidence that rate of consumption varies with temperature. In general there appears to be an optimum temperature for maximum consumption, at least in the few species which have been adequately studied. This optimal range is evidently correlated with the summer temperatures prevailing in the natural habitat of the species concerned. Komarova's (1939) picture of the stomach contents of the long rough dab of the Barents Sea shows an increase in "index of fulness" from 0° to a maximum at 1° C., beyond which there is a very sharp drop, to about 10 percent of the maximum at 4°. On the basis of daily consumption, some part of this decrease might be discounted as the result of more rapid digestion, but the optimal point would be little changed. In Pentelov's (1939) experiments, brown trout given access to unlimited food increased their consumption with increase in temperature up to 15° C.; but thereafter there was a decrease in average consumption, accompanied by greatly increased variation, from week to week. Arnoldi and Fortunatova (1937) determined experimentally that the maximum rate of feeding of *Gobius*, *Scorpaena* and

other Black Sea fishes was between 18° and 20° C., followed by a rather sharp decrease at 22°. For our largemouth bass the optimum range is apparently even higher. Markus (1933), using temperatures from 4° to 34° found that with rise in temperature the ration increased, up to 28°. Between 28° and 34° there was no significant change, though the difference observed was a decrease in the case of the larger fish used.

Hathaway (1927) has made other interesting observations. Using pumpkinseeds, bluegills and largemouth bass, he found that the food consumed by fully adapted individuals at 20° was up to 7 times as great as that consumed at 10°. The greatest difference was exhibited by the bluegill, and it is probably more than a coincidence that this species does not occur as far north as do the other two. Among the pumpkinseeds, individuals of 14 grams weight showed greater temperature differences (5:1) than those of 44-87 grams (about 3:1). Another important effect demonstrated by Hathaway was that after transferring the fish from the higher to the lower temperature, or vice versa, it took two or three weeks for the rate of feeding characteristic of that temperature to be attained. A similar effect of pre-conditioning on rate of digestion has been observed by Riddle (1909) for the bowfin.

#### QUANTITY OF FOOD AVAILABLE

It is perhaps obvious that food available should have an effect on rate of feeding. For any given environmental conditions, there is a maximum amount which will be taken, regardless of how much is available, though this maximum varies greatly with the individual fish. It also varies with the previous history of the fish—whether it has been well-fed or poorly fed (Moore 1941), the latter exhibiting the greater appetite. At levels well below the maximum ration there is some evidence that feeding on a preferred food object is in proportion to availability. Thus Ricker (1941) found that the frequency of occurrence and average number of young sockeye salmon found in stomachs of cut-throat trout, coho salmon and squawfish, in different years, was in direct proportion to the numerical abundance of the sockeye in the lake. Ivlev (1945a) has made a more exact study, and finds that, with increasing availability of food  $p$ , the daily ration  $r$  approaches the maximum ration  $R$  according to the formula:

$$r = R(1 - e^{-\xi p}),$$

where  $\xi$  is a constant. This was confirmed in experiments on the carp, roach and bleak.

Another type of evidence concerning food consumption comes from data on rate of growth in relation to population numbers. Swingle & Smith (1942), among others, have published semi-quantitative data on this phenomenon, which is familiar to everyone who raises pond fish. Over a fairly wide range of population densities they found a tendency for yield of bluegills to be fairly constant in ponds fertilized in a given manner. This presumably means that at the higher densities the fish consume less food

per individual, which is reflected in their slow growth. Data from nature, on the same point, include Foerster's (1944) observations on the rate of growth of young sockeye salmon in populations of different sizes in a lake; there was a marked inverse correlation between rate of growth and population, at least above a certain threshold level of the latter.

#### CROWDING

Data of the sort mentioned in the preceding paragraph are to be interpreted with a proviso, in view of the possibility that population density itself may affect food consumption, independently of availability. Claims for the existence of such a "space-factor" have been made by a number of investigators (Willer 1929). Evidence has been adduced by Willer that rather dense crowding of trout will decrease rate of growth even when food supply is kept constant, though it is not clear whether food consumption is reduced or whether there occurs a decrease in efficiency of utilization of food for growth. However, a simple experiment by Nikolsky and Kukushkin (1943) suggests that this may not be an invariable rule, for speckled bullheads increased their food consumption when in a group, while goldfish decreased theirs. The question evidently needs much additional study, which, from the point of view of production, must include a demonstration that the densities which produce the observed effects normally occur in nature.

#### SIZE OF FISH

Determinations of effects of size on rate of feeding are difficult because of many possibilities of error. It is essential that availability of food be the same for the two sizes being compared, and, considering that for each size of fish there is presumably a most attractive size or kind of food, equalization presents difficulties. It is desirable too that the fish used be of a fairly uniform stock, and above all, that selection be avoided. The large and small fish used should not be the faster- and slower-growing members, respectively, of a single population—as was the case, apparently, in the experiments of Markus (1933). Whether any really rigorously controlled experiments have been made is perhaps doubtful. However, there are many indications that larger fish tend to eat less than smaller ones, per unit body weight.

Pearse (1924) found that at 19° small pumpkinseeds and rock bass ate a much larger ration, per unit weight, than did larger ones. Among bullheads and bass however, the difference was small and probably not significant; in the latter it favored the larger fish. Hathaway (1927) discovered that the daily ration eaten, per unit weight, decreased among fully fed pumpkinseeds held at 20° in aquaria, from about 6% at a weight of 14 grams to 1.4% at 87 grams. Arnoldi & Fortunatova (1937) found that large *Scorpaena porcus*, given excess food, ate 1.7% of their weight daily, while small specimens ate 3.0%. Similar but more qualitative observations have been published for yellow perch by Pearse & Achtenberg (1920), and for largemouth bass by

Thompson (1941). Even the data of Markus (1933) are useful, for he found that the smaller bass (30-54 grams) ate more per unit weight than the larger ones (121-200 grams), in spite of the fact that the latter had been the faster-growing members of the brood.

Observations on stomach contents of wild fish suggest the same story. There are very few exceptions to the rule that large fish more often have empty stomachs than do smaller ones of the same species; or more generally, that the average stomach content, per unit body weight, is less among large fish. In this connection it should be remembered that the smaller fish might tend to digest their food more rapidly than the larger, since digestion is a function of surface rather than of volume, so that the observed differences in quantity probably do not tell the whole story. An exception must be made for the very young individuals of some (all?) species, which seem slow to begin really active feeding (Einsle 1944, Ricker & Foerster MS).

#### OTHER EFFECTS

That the process of reproduction often interferes with the normal feeding of fishes is a common observation, the degree of change varying, with the species, up to almost complete cessation in some cases. Rhythms of feeding within a 24-hour period have been discovered by a number of investigators. For example, Zadulskaja & Smirnov (1939) investigated the feeding of Barents Sea cod in relation to the time of day, the stage of the tide, and the interaction of these two. Ivlev (1945a) found that when food was distributed in aggregations, instead of uniformly, it affected the regularity of the relationship, cited earlier, between the quantity of food available and the daily ration, and he has devised a formula which describes the discrepancy in terms of the amount of aggregation.

#### UTILIZATION OF FOOD ORGANISMS

The determination of the ecotrophic coefficient—the fraction of the production of a food organism which is actually consumed, in our case by fish—is, as Ivlev has emphasized, the most difficult of all the problems involved in productivity studies. In Borutsky's (1939) balance sheet for *Chironomus plumosus* in Lake Beloe, 440 kilograms dry weight, or 46 percent<sup>1</sup> of the net production, is assigned to consumption by water animals, among which fishes apparently predominate. This figure is obtained by subtraction rather than by direct quantitative observation on the food of the fishes of the lake, and a confirmation from that source would be very desirable. Nevertheless this estimate and Borutsky's estimates for other benthic animals are possibly the only attempts to obtain this information, which are satisfactory even in theory. Other similar attempts (e.g. Okul 1941, 1941a, Lindeman 1942) are weak

<sup>1</sup> This percentage is apparently larger than an average over a period of years would be, because during the year of Borutsky's observations the *Chironomus* population exhibited a net decrease to about half its original size.



because estimates of invertebrate production are inadequate—no account is taken of non-predatory mortality in estimating the latter. To indicate the possible importance of such mortality, Borutsky estimates that the total annual consumption of *Chironomus plumosus* within Lake Beloe was 440 kilograms dry weight, as compared with 855 kilograms which died "naturally." For Corethra, Tanypinae, and Oligochaeta the disproportion was much greater, 9 kilograms as compared with 922 in the case of the last-mentioned.

Obviously there must be more determinations of what the production of invertebrate animals really is in different situations, before it will be possible to have definite information on what fraction of that production is used by fishes. Borutsky's methods, if checked as suggested above, seem the best yet devised for the bottom fauna. Okul suggests that a possible basis for the estimation of the non-predatory mortality of plankton foods has been laid in Kastalskaia-Karzinkina's (1935) criteria for distinguishing dead from living plankters in preserved collections, presumably to be used in combination with experimental information on the time required for these organisms to disintegrate or to fall to the bottom. The mortality estimated in this way, combined with estimates of consumption by fishes, would provide an estimate of total mortality and hence total production, with which the fishes' consumption could be compared in order to obtain the ecotrophic coefficient.

Where the data necessary to estimate the absolute magnitude of the ecotrophic coefficient are lacking, several attempts have been made to determine its relative size for different foods, so that potential fish production can be more accurately estimated from standing crop data. This has been done for a New York stream by Hess & Swartz (1940), using the blacknose dace as the feeding animal. The percentage frequency of occurrence of each food item in the dace stomachs was divided by its percentage occurrence in the stream to obtain a "forage ratio." The product of the mean density of an organism per square foot and the forage ratio is the "food grade value" of the organism in the stream, except that (for reasons not explained) forage ratios greater than unity were considered as unity for this purpose. The method of Hess and Swartz is similar to that of Shorygin (1939), who calculated an "index of food preference" for the various gobies of the North Caspian. This index is the percentage weight of a given type of food in the alimentary canal, divided by the percentage weight of the same in the whole bottom fauna of the feeding grounds. In this way he discovered that crustaceans are eaten relatively much more frequently by gobies than are molluscs or worms.

One factor not considered in either of the above studies is the relative rate of digestion of different types of food. It has commonly been supposed that small or soft-bodied organisms are digested by fishes more rapidly than larger or thick-skinned types. This

has been demonstrated for different kinds of immature insects fed to brook trout, by Hess & Rainwater (1939). Similarly Karpevich (1941) found that Gammaridae were digested more rapidly by three marine fishes than were larger crustaceans or small fishes. Even where such relationships have not actually been demonstrated, they have sometimes been assumed and attempts made to take them into consideration in a semi-quantitative manner. Tester (1932) did so graphically, constructing rectangles to represent the relative importance of each different kind of food by using its volume percentage representation in the total food as the horizontal dimension, and its frequency of occurrence (percentage of stomachs which contained it) as the vertical one. Because he felt that volume was more important than frequency, the vertical scale was made only 40 percent of the horizontal one. A similar principle has been introduced by Komarova (1939). An "index of fullness" is computed as the ratio of the weight of a given kind of food in the stomach to the weight of the fish, the whole multiplied by 10,000. As a second index, the percentage of stomachs which contain that food is computed, and the geometric mean of the two indices is called the "index of significance" for the food in question. In addition, an "index of density" for each bottom organism was similarly constructed, as the geometric mean of its biomass in grams per square meter and its percentage frequency of occurrence in the samples taken. The ratio of the "index of significance" to the "index of density" constituted a measure of the availability and/or desirability of the food in question. In this way Komarova, for example, showed that the long rough dab of the Barents Sea "preferred" Ophiura and Peeten, but rejected the abundant Astarte.

While schemes of this sort may have considerable utility, they seem incapable of presenting any very accurate picture of the relative value to fishes of the different foods in an environment. In the methods of the last paragraph, the relative importance of bulk and frequency must be rather arbitrarily fixed, and the two authors quoted do not agree on their respective weights. Even if this be done satisfactorily, there may be situations where the observed utilization of different foods varies. Thus the writer (1941) found that the piscivorous fishes of Cultus Lake ate little but sockeye when the latter were abundant, but in years when sockeye were scarce they greatly increased their consumption of other fishes and insects. The estimated "value" of the latter foods, as determined by their relative occurrence in the stomachs, would thus vary a great deal from year to year, even though their abundance did not change. However the situation in which this was observed was rather unusual because of the sharp changes which occurred, from year to year, in the abundance of the preferred food.

In streams the variables affecting utilization of different foods include the temperature of the water and changes in its level, both of which Ide (1942) showed to be very important in determining the con-

sumption of different stream insects by speckled trout. Hence studies made, for example, during a year of high water levels or constant water levels might give quite a different picture of relative utility from studies made when levels were low, or were variable. Leonard (1939), Mottley *et al.* (1939), Denham (1938) and others have shown the effect of floods in changing the fauna of a stream, and also the great variability which exists between individual samples. In view of these and other complexities one may wonder whether the effort required to get any useful picture of fish-supporting capacity from benthic invertebrate organisms, in so variable an aquatic habitat as a stream, may not be beyond the limits of practicability.

Even apart from estimates of crop or production, the determination of the quantity of food consumed by the fish in a body of water is full of interest. Such estimates can be based upon comprehensive observations of actual stomach contents, and upon experimental data on the rate of digestion under conditions simulating the natural as regards temperature, amount of food and so on. Unfortunately relatively few investigators have made an effort to combine these two types of data. Less satisfactory information can be had by combining the results of ordinary food studies with more-or-less plausible guesses concerning rate of digestion. In some instances estimates of the daily ration can be combined with data on the size of the stock of the fish in question, to give a picture of total consumption for a year:

a. *Plankton-eaters.* Okul (1941a) studied the plankton-eating fishes of the Sea of Azov, including the anchovy, the *tiulka* and three others, and determined the rate of digestion at the temperatures prevailing throughout the year. Combining this with observations on the stomach contents of wild fish, he showed that the daily ration of the anchovy, for example, was 0.8-1.0% of the body weight, in summer; for the *tiulka* it was 0.6-0.8%. For the whole year it was 9.5 times the mean weight for the anchovy and 7.7 times that of the *tiulka*. Combining this with estimates of the total stock of these fish made by Maisky and Smirnov, he computes the total annual consumption of plankton as 920,000 metric tons by the anchovy and 600,000 tons by the *tiulka*. Allowing 10% for the less important species, the total is 1.7 million tons of plankton consumed in the whole Sea, or 42 tons per square kilometer (wet weight).

Much greater rates of feeding than the above were discovered by Sushkina (1942) for fingerlings of the Caspian shad in the Volga River near Saratov. Fish from 25 to 50 millimeters long consumed 11% of their body weight daily, chiefly Cladocera and Copepoda.

b. *Benthos-eaters.* Probably the earliest exact study of food consumption in nature was that of Arnoldi (1929). The trout of the Armenian Lake

Goehka apparently eat little but Gammarus, and do their feeding at regular hours. These favorable circumstances were exploited by Arnoldi, who determined that the mean daily ration was 1.7-2.0% of the body weight, while the maximum for the population was 3.1%. Krivobok's (1942) study of the feeding of year-old bream in Lake Glubokee extended throughout the warm months of the year. He found the daily ration to be 4.3% of the body weight early in May, 10% during summer, and it fell to 6% by early September. The food eaten consisted chiefly of midges and littoral Cladocera and Copepoda, so should be classified as a mixture of plankton and benthos. Apparently no estimate of the total population of young bream was available.

Ivlev's (1939) determination of the food of year-old carp does not apply to a strictly natural situation, but to one of a type which is of much importance nevertheless—a pond used for fish-culture, 0.25 hectare in area. His methods were somewhat different from those described above. He determined the nitrogen content of the metabolic products (urea, etc.), that of the faeces, and that of the new body substance. The sum of these, converted by means of a nitrogen-caloric coefficient, gave the total food consumed in terms of its heat of combustion. At the same time, examination of food tract samples provided qualitative data on the food consumed, which was almost wholly insects, chiefly chironomids. He found that each day the carp consumed food equivalent to 16.0% of their body substance at the start of summer, decreasing to 4.3% at the end. The large initial rate of consumption is probably related, in part at least, to the rather small amount of stock present: 160 individuals weighing 2.2 kilograms. By the end of the experiment however, they had increased to 67.4 kilograms. The total consumption for the season was  $2.93 \times 10^8$  gram-calories, corresponding to about 520 kilograms of food wet-weight, or 210 tons per square kilometer.

c. *Fish-eaters.* Maisky's (1939) study of the piscivorous fishes of the Sea of Azov showed that the sander was the principal predator, the sheatfish and others being of some importance. The monthly rate of fish consumption by sanders in the Caspian Sea was estimated by A. F. Karpevich<sup>2</sup> from data on stomach contents and rate of digestion, and varied from zero during five winter months to 1.5 times the body weight, in summer: i.e. a daily ration of 5%. The mean was 0.58 per month, or nearly 7.0 per year, considering the stock as a whole. In default of information on the Azov sanders this figure was combined by Maisky with his own and Boiko's estimates of the total sander population of the Sea of Azov, to give their total yearly consumption of fish as 309,000 metric tons round weight or about 7.8 tons per square kilometer.

<sup>2</sup> Karpevich's work is cited by Maisky as a MS, 1937. From its title: "Daily and yearly utilization of natural foods by fishes," it appears that the food consumption of a number of additional species is included.

## CONVERSION OF FOOD TO BODY SUBSTANCE

Ivlev (1939, 1945), following Terroine, uses the following classification of the disposition of the total energy,  $Q$ , in the food consumed by an animal:

$Q_R$ : energy in material not absorbed by the alimentary canal.

$Q_t$ : energy of "primary heat" or basal metabolism.

$Q_v$ : energy of external work.

$Q_w$ : energy of internal work.

$Q'$ : energy accumulated in growth.

For our purposes the three energies  $Q_t$ ,  $Q_v$  and  $Q_w$  can be considered together as "respiration," that is, the total energy used in the normal course of a fish's day-to-day activities; leaving  $Q'$ , out of the  $Q - Q_R$  absorbed, for increase in bulk.

To present the results of experiments clearly and concisely, two principal ratios are used:

$K_1 = \frac{Q'}{Q}$ , the energy coefficient of growth of the first order, is the ratio of growth to food consumed.

$K_2 = \frac{Q'}{Q - Q_R}$ , the energy coefficient of growth of the second order, is the ratio of growth to assimilation (food digested and absorbed).

The second of these coefficients has also been designated the AEE coefficient. Lindeman (1942) makes use of a "respiratory coefficient," which is  $(Q - Q_R - Q')/Q'$  in the symbols above, and can easily be converted to the second-order coefficient of Ivlev. While to express the above coefficients in energy terms is certainly best, in many studies only the weights of food and of feeder are given, so that in what follows it will usually be necessary to speak in terms of the corresponding weight coefficients.

Some investigators have taken special pains to determine the magnitude of the "maintenance ration," which is the food consumed when the fish neither gains nor loses weight (Dawes, 1930-31; Pentelow, 1939; Moore, 1941). However for problems of production this quantity has no special interest; rather it is only one point on a graph of efficiency of food conversion against amount consumed, all of whose points interest us equally.

In assessing the utilization of food by fishes, we will be interested principally in the first-order coefficient  $Q'/Q$ . The various factors which may influence the efficiency of conversion of food to fish flesh must be considered individually. First however it will be useful to review some studies of the efficiency of digestion and assimilation of different foods, that is, determinations of the ratio  $(Q - Q_R)/Q$ , since this is obviously involved in the former question.

### ASSIMILATION OF FOOD EATEN

Direct determinations of percentage utilization of foods by fish have been made by comparing the dry weight, the calorific value, or the nitrogen content of

the food with that of the faeces, over a period of time. Such tests have been made by Karzinkin (1935a, 1939) in aquaria using young pike as the experimental animal, and by Iablonskaia (1935) using carp, for almost all the important types of fish food found in fresh waters. Ivlev's (1939) experiments give the same information for carp feeding under natural conditions in ponds. Arnoldi and Fortunatova (1937) have some data for several marine species. In general, assimilation is rather efficient, attaining 80-90% for most food animals, but falling lower among those which have extensive hard parts. While the assimilability of different components of the food is not uniform, that of fats being lower than that of carbohydrates (Ivlev 1939b), this fact is not usually important because most aquatic foods are of a rather uniform composition, and hence their dry weight gives a good idea of their food value (Ivlev 1945), though naturally extensive calcareous or chitinous hard parts would be a disturbing item.

Assimilation is also to some degree affected by external conditions. Arnoldi and Fortunatova found that *Gobius cephalarges* assimilated 88-89% of its food at 19°, but only 74-75% at 12°. Similarly Karzinkin (1935) found a tendency for fingerling carp to assimilate less as temperature decreased, from about 80% at 21° to 70% at 10°. Scarcity of oxygen in the water had a similar effect. In the same study the amount of food eaten was found to be of some importance; in one series, sparingly-fed carp absorbed 90 percent of their food (*Chironomus* larvae), while those given a lot of food absorbed only 78%. This was attributable partly, at least, to the fact that the earlier part of a large meal remained in the food canal a shorter time and was less completely absorbed than was the later part.

### EFFECT OF AGE

We turn now to a discussion of factors governing what fraction of the ration will be used for production, or in other words growth. Considering first the one which Ivlev says is most important of all, the age of the animal concerned, it is disconcerting to find little available factual information for fishes. Ivlev's (1938) studies with several *invertebrates* indicate a sharp drop in the energy coefficient of the second order, from 43-44%<sup>3</sup> in the very young

<sup>3</sup> In a preliminary series of experiments using very young *Tubifex* worms (Ivlev 1939c), the second-order coefficient ( $K_2$ ) was found to be 60%, as compared with 42% for the same stage of the same worms as reported in the 1938 paper. Ivlev apparently does not comment on the discrepancy; in the earlier (1939c) series the density of the worms was adjusted to the optimum number for most rapid growth, while in the later (1938) experiment this point is not mentioned, though it is stated that the worms grew less rapidly than in nature. Possibly therefore differences of density account for the discrepancy, though it seems odd that there should be so large an effect of this sort, in view of the constancy of the initial value of  $K_2$  for four very different types of organisms, as reported in 1938. The point is of some importance because Lindeman (1942) compared the large 1939 figure (made slightly larger by an error of transcription) with an estimated  $K_2$  of 42% for fishes, as part of the evidence which might "reflect a trophic principle of wide application: the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle." Even if a  $K_2$  value as high as 60% is actually sometimes achieved by very young *Tubifex*, Ivlev's later studies show that all lower values down to zero are found among the older worms and among several other invertebrates.

to zero when growth ceases. That a similar falling-off occurs among warm-blooded animals, all of which have determinate growth, is of course obvious. For fishes too such a decline seems very probable in spite of the fact that growth is indeterminate in most species. The quantitative study of its course among important food or game species is a research problem which should be given immediate attention. Most of the existing information pertains to rather small individuals, and in no case does there appear to be a really good comparison between old and young of the same species.

To summarize briefly some of the data available, Scholz (1932) found that age I pike, fed on fish under near-optimum conditions, had  $K_1$  coefficients of about 33% on the average (29-36%), as did some of the larger pike at age 0—all on a weight basis. A single age II pike had  $K_1 = 18\%$ , and one of age III had  $K_1 = 26\%$ . Because of the small number of older fish, these results can, at most, suggest that a fall in  $K_1$  occurs with increase in age. Older fish were used by Brofeldt (1927), who found an average  $K_1$  of 8.5% through summer and early autumn, for 8 pike of age IV, fed on excess fish. Possible sources of error in this experiment have been mentioned by Scholz, so that the result is not conclusive, but it does lie in the direction suggested by his own work with older specimens. Karzinkin (1939) fed age 0 pike on various natural foods, and obtained  $K_1$  values of 24-27% under optimum conditions. When foods too small for the size of the fish at any given time were used, this percentage fell off sharply. The pike used varied from 9 to 80 days in age, and there was some tendency for  $K_1$  to be less, during the first 10 or 20 days of this period, than it was later. Pentelow (1939) obtained  $K_1$  values up to about 29% for young brown trout fed on Gammarus. Another series of experiments which used a natural food was made by Dawes (1930-31), who fed two-year-old plaice on the mussel *Mytilus edulis*. The principal impression one gets from this long study is of the tremendous variability between individual fish. The  $K_1$  values for plaice which were fed all they would eat were rarely greater than 10%, and averaged considerably less—certainly much less than found for Karzinkin's or Pentelow's younger fish. There may also be a significant difference between smaller and larger fish within Dawes' own data, but the absence of any general summary from this point of view, and the possibility of temperature effects, makes it difficult to be sure.

A considerable body of work has been done on the

As shown below, fishes too apparently exhibit a similar range of  $K_2$  values, from about 45% down to something not far from zero. Hence to discover characteristically different values of  $K_2$  for "primary" as compared with "secondary" consumers would be a very complex ecological problem. This is not to say that such an effect does not exist, but the removal of this part of the factual evidence leaves Lindeman's hypothesis with very shaky foundations, even if only temporarily. Had he lived, the brilliant author of the hypothesis would certainly have made this discovery himself, and might by now have remedied the situation. In any event Lindeman's "corrections for respiration," for invertebrates and probably fishes also, are several times too small to be representative of populations of mixed ages, living under conditions which must, on the average, be something short of optimal.

efficiency of artificial foods in making fish grow, but again without critical comparisons by age or size. For example Detweiler (1931), using brook trout fingerlings, obtained first-order coefficients of 25-27% for beef heart and liver, and Moore (1941) obtained a figure as high as 48% for liver fed to green sunfish. In terms of weight, we should of course expect rather higher coefficients from these than from natural foods, because of their smaller content of indigestible matter.

#### EFFECT OF AMOUNT OF FOOD CONSUMED

Inasmuch as a certain minimum basic ration is necessary for a fish to maintain its weight, it must be expected that increase in consumption for some distance beyond that level will result in an increased fraction of food being devoted to growth. Pentelow's summary of his observations on brown trout (1939, Fig. 6) shows that at temperatures between 5° and 10° efficiency increased in an approximately linear manner with increased consumption: the maximum daily ration taken was about 6% of the body weight, and this corresponded to the maximum efficiency of conversion—about 29%. At higher temperatures the same trend existed, but the data were more irregular, and the conversion efficiency of any given ration averaged less.

In Pentelow's experiments little indication was obtained of a decrease in efficiency of utilization at very high rates of feeding. However, Dawes (1930-31) has some evidence that plaice fed an "intermediate" ration use it more efficiently for growth than those fed the maximum ration. An effect of this sort might perhaps have been expected on the basis of Karzinkin's observation mentioned earlier, that assimilation is less complete when large amounts of food are eaten; though that would not be the only possible cause. The same effect is indicated in a graph by Thompson (1941), which summarizes a number of experiments on largemouth bass fed on minnows at 21°; though unfortunately the observations on which it is based remain unpublished. Taken at face value, the graph indicates that the maximum coefficient of growth ( $Q'/Q = 40\%$ ) is attained when the daily ration is 3 to 4% of the body weight.

#### EFFECT OF TEMPERATURE

No experiments appear to have been performed in which the effect of temperature upon the coefficient  $K_1$  or  $K_2$  can be completely distinguished from other factors, especially amount of food taken. Some of Pentelow's brown trout (1939, Fig. 3) do appear to have utilized food less efficiently ( $K_1$  decreased) at the higher temperatures, in the absence of any striking change in amount eaten. However they were not held at such temperatures long enough to eliminate possible preconditioning effects.

Experiments and observations are fairly numerous, in which the effect of temperature upon efficiency may have been direct or may have been the result of increased food consumption. In Ivlev's experiments (1939) the best utilization of food for growth by yearling carp (46%) occurred during the



warmest month of the summer (average water temperature 23-24°). Similarly, in Krivobok's (1942) analogous study of the bream, best conversion of food to flesh occurred when the temperature reached 21°. When temperatures fall below a certain salubrious range, it may be impossible for a fish even to maintain its weight, much less grow, even though food be available in abundance. This was observed by Dawes (1930-31) among plaice whenever water temperatures fell below 10°, and by Markus (1933) among largemouth bass held at about 4°. The Murman herring of the Barents Sea were observed by Manteufel (1941) to lose weight and decrease in fat content during winter. Whether because of temperature directly or failure to feed, it seems likely that such effects may be fairly general, though the exact temperature range throughout which growth is impossible must vary with the species and even the population concerned. It should be noticed that neither the plaice nor the herring above ceased feeding entirely in winter, though the quantity of food taken was greatly reduced.

#### EFFECT OF FASTING

Ivlev (1939a) shows that young pike, after fasting for up to 20 days, utilized food more efficiently afterward than did non-starved pike. Pentelow (1939) noted that his brown trout grew more rapidly after being fed a restricted diet than did those which were continuously given all the food they would eat, though here the increase might have been partly or wholly due to increased food consumption.

#### DIRECT ESTIMATION OF FISH PRODUCTION

The instantaneous rates postulated by Clarke (MS) to describe the production of an organism are:

- A—rate of assimilation of food
- R—rate of respiration
- D—rate of decomposition (fraction of the organisms which die a "natural" death)
- C—rate of consumption by other organisms

For the purpose of computing the production of fish populations it is convenient to combine these as follows:

$$k = A - R = \text{rate of growth.}$$

$$i = D + C = \text{rate of mortality.}$$

In some fish populations these two statistics can be estimated with fair accuracy, using standard methods of investigation (Ricker 1945). That is, the age of the fish and hence the rate of growth can be estimated from markings on hard parts (scales, otoliths, cleithrum, opercle, fin rays, etc.) in representative samples; and the mortality rate can be computed from the abundance of successive age-groups in a series of representative samples, or from recaptures of marked fish. These methods give the rates of growth and mortality from one year to the next.

In addition, it is of course necessary to have in-

formation on the weight of the stock present, of the given age-group(s), at some time during the year for which production is being computed. At times this can be obtained by direct enumeration, but more usually an indirect approach is necessary. Petersen's mark-and-recapture method is usually employed, or Schnabel's modification of it (Ricker 1945a, b).

Given the above information, a first or approximate estimate of production can be made by assuming that the growth and mortality are similarly distributed seasonally. The rate  $k-i$  represents the instantaneous rate of increase or decrease of a unit weight of stock at any instant of time. Letting  $P$  represent the weight of the stock (biomass) at any time  $t$  in years, its rate of change in size is given by:

$$\frac{dP}{dt} = (k - i)P.$$

Integrating,

$$P = P_0 e^{(k-i)t},$$

where  $P_0$  was the weight of the stock at time  $t = 0$ . The average biomass,  $\bar{P}$ , present during the year, is given by:

$$\begin{aligned} \bar{P} &= \int_0^1 P_0 e^{(k-i)t} dt \\ &= \frac{P_0 (e^{k-i} - 1)}{k-i} \end{aligned}$$

The growth or production during each  $n$ th of the year will be  $k/n$  times the population present at that time. The sum of these for every  $n$ th is the total production  $B$  for the year, and this is equal to  $k$  times the average population during the year:

$$B = \frac{k P_0 (e^{k-i} - 1)}{k-i}$$

This expression is equivalent to formula (11) of the appendix of Clarke's (MS) work, with  $t = 1$  year. To obtain the total production for the species, the production of all age-groups must be summed. In practice, it is rarely that the youngest age-group or groups—those of less than the usual usable size range—can be treated in this way, because while their rate of growth may be known, their mortality rate is unusually difficult to obtain in nature.

A computation on the above plan will be correct only if growth and mortality are similarly distributed seasonally. Hence one other piece of information is necessary for a really accurate estimate of production—namely, the actual or relative seasonal distributions of growth and of mortality. Although most growth studies yield estimates of size at intervals no shorter than a year, the seasonal distribution of growth has been worked out for a number of fishes: for example whitefish (Hart 1932), ciscoes



(Fry 1937), squawfish and sockeye salmon (Ricker 1938), yellow perch (Langford & Martin 1941), *Blaufelchen* (Elster 1944), to name only a few. Most of such estimates are for the younger fish only of the population, because it is no easy task to obtain and examine sufficiently large samples of the older fish to give a reliable estimate of rate of growth within a year. In temperate climates growth tends to fall to zero in winter, even though the feeding of the fish need not necessarily cease. There may also be a period of slow growth in summer for fishes then living at temperatures greater than the optimum range to which they are adapted, though to date this appears to be only a possibility based on experimental studies of feeding, rather than on actual observation in nature.

The seasonal distribution of mortality is not ordinarily known, except where mortality is largely the result of fishing and hence susceptible to observation. Where there exists a large non-fishing mortality, such as was demonstrated in some small lakes for bluegills and other warm-water fishes (Ricker 1945a, c), it is not easy to estimate its seasonal incidence. In general it too will probably vary seasonally in something the same way as growth, but possible unfavorable effects of the spawning season or of extreme winter conditions cannot be overlooked. Also, that part of the natural mortality which is the result of predation will probably not fall to zero in winter, in the way growth appears to, because even the cold-blooded predators (or at least some of them) do eat during winter to some extent; while warm-blooded predators are of course as active in winter as in summer, if possibly less numerous.

In spite of these objections, often the only way to get a first estimate of production will be to assume that mortality and growth are proportional throughout the year. There are however some interesting examples of actual estimates of seasonal mortality rate throughout the year, for very young fish. Under favorable circumstances pelagic larvae can be sampled quantitatively using plankton nets, from which estimates are made of their abundance from week to week, as has been done for the mackerel of the east coast of North America by Sette (1943). A marking technique has been used by Foerster (1938) to obtain the same information for fingerling sockeye salmon. Both these studies indicate an unusually large mortality among the fish shortly after free-swimming life has begun, and hence neither is likely to be directly applicable to the older fish of the same species. The method of computing production when  $k$  and  $i$  vary seasonally is essentially the same as when they are in proportion throughout the year, only the production must be computed at rather short intervals of time, using the values of  $k$  and  $i$  appropriate to the season, and the whole added to get the total production. An example has been given by Ricker & Foerster (MS).

For fishes of kinds or sizes for which the obtaining of quantitative samples of the stock at frequent intervals is impractical, and which lack the migratory

habit that made Foerster's method feasible, we are still at loss to evaluate seasonal mortality. Pond experiments would seem to offer attractive opportunities.

### YIELD

For man, it is not enough that fish should be *produced* in a body of water; he is interested principally in *using* them. In general the *yield* of fish will depend upon their production, and also on the effort put into their capture. However, the fact that some fish are taken by man can in itself affect production, so an examination of the effects of fishing on a fish stock is of much importance.

### EFFECTS OF EXPLOITATION

The most universal effect of fishing is perhaps a change in the age composition of the commercial stock. (Fish which are caught only just prior to their imminent natural death, are an important exception.) Even a rather small amount of fishing may suffice to produce a considerable change of this sort, in a long-lived fish (Baranov 1918, Thompson & Bell 1934). Imagine a stock which is vulnerable to fishing for ten years of the life of the fish—say from age VI through age XV. Let the annual natural mortality rate be 20%, in which event the number of XV year fish will be  $(0.80)^{10} = 11\%$  of the number at age VI. Suppose now a fishery begins to operate, which would take an additional 20% of the stock each year—and that will seem to the fisherman a very modest amount. Taking into account a small amount of competition between the two kinds of mortality, the new total mortality rate will be about 36%, and, after enough years elapse to spread the effects of fishing through the stock, the age XV fish will number only  $(0.64)^{10} = 1.2\%$  of those of age VI. Thus there is a marked decrease in the relative number of the oldest and largest fish, even at rather light fishing intensities. It is probably this effect more than any other which accounts for the popular impression that fishing in the good old days was far better than at present. In general it was, in the sense that large fish were relatively more numerous, and may also have been easier to catch. But the total catch under those conditions was not necessarily greater than at present, and may have been much less.

How far back it is necessary to go to find this more primitive age distribution will vary with the locality and the kind of fish. For most North American waters and fishes, the change has occurred to a large extent within the memory of men now living; the same is true of many sea fisheries throughout the world, which have attained important proportions only since boats and gear have become mechanized. In old-world fisheries subjected to centuries of exploitation the change occurred long ago, but even there it is occasionally possible to get some idea of the primitive age distribution. Nikolsky (1937) examined fish bones from a Kuban River village site of the Hellenistic Age (ca. 350 B.C.), and found

that the carp and sheatfish were much larger and older than in modern catches.

The decimation of the ranks of the oldest individuals may have a serious effect upon a fish stock, if maturity of the fish is late in arriving. That is, reproduction may be curtailed to a point where a progressive decline in abundance sets in. Unfortunately examples of this event are not too well documented, but there are situations where it seems very likely to have happened. This is true of such species as the sturgeon and maskinonge of our Great Lakes, which, after briefly supporting a large fishery, are now commercially extinct or nearly so. The same is true of the once-abundant whitefish populations of the Canadian lakes Winnipegosis and Manitoba.

Since fishing inevitably results in a marked reduction in the relative number of large breeding individuals in a stock, it may be asked why the near-extinction of fish stocks by fishing is not more common than it appears to be. There must be important compensating factors. The most obvious of these is the fact that the efficiency of reproduction and the survival rate of young fish tends to increase as the number of spawners decreases. This can be postulated as a general law of reproduction on theoretical grounds (Nicholson 1933), but there are also direct observations supporting it: for pink salmon by Pritchard (1939), and for haddock by Herrington (1944). Aside from this, numerous investigators have concluded that reproduction is ample even under conditions of rather intensive exploitation, simply from the fact that the yield of their particular fisheries does not decrease. This is apparently true of most North Sea species and also of the very important California sardine, whose catch, in spite of misgivings, has stubbornly refused to decline, partly because recruitment is now actually greater than formerly (Silliman 1943).

Another important effect of fishing may sometimes be demonstrated in the rate of growth of the fish concerned: that is, with reduction of the stock on hand there comes a noticeable increase in the rate of growth of the individual fish. This may be simply because, with the reduced stock, more food is available per fish, or there might also be an actual increase in production of food organisms. The latter situation would arise if the fish's feeding exerted a controlling influence on the abundance of its prey, and a relief from predation, at possibly a critical stage, would make for a great increase in production of the food organism. Such questions are a part of the general question of what factors limit the production or standing crop of aquatic organisms, a subject which is still very obscure. However, Manteufel (1941) has evidence that the Barents Sea herring can and do produce local depletions of the crop of *Calanus* at certain times of the year, while in the restricted habitat of bays this food may be practically exterminated.

Whatever the exact factors involved, an inverse relationship between the abundance of fish and their rate of growth has often been observed. It has been

detected by comparing year-classes of different "strengths" among ciscoes (Hile 1936), haddock (Anderson 1938), pink salmon (Davidson & Vaughn 1941), sockeye salmon (Foerster 1944), and many others. Hile's paper contains a review of a part of the rather extensive literature on this topic. The same relationship is also apparent when a species has declined over a period of years, an effect which is most likely to be marked in waters where reproduction is for one reason or another poor. Thus in the western Baltic Sea and adjacent waters marine species like the plaice live well, but do not reproduce. The early fishing-up of the stock of these fish resulted in an amazing increase in rate of growth, since immigration was insufficient to maintain a dense population on the grounds (Petersen 1922, Molander 1938). It must not be thought, however, that growth and stock are invariably inversely related. Such an effect is not to be expected where a fish, even when most numerous, eats only a small part of the food available to it, as is apparently the situation with the *Blaufelchen* of the Bodensee (Elster 1944). Nor will it be found where a species is only one of the less important of a number of fishes feeding on a common food.

Even without an actual increase in rate of growth at a given age, the introduction of fishing may result in an increased rate of production of the species as a whole. This is because the stock under conditions of exploitation contains a relatively much larger number and weight of younger fish, and as we have seen, younger fish utilize food more efficiently. This makes possible a larger production of fish in a given environment, and hence greater yield, provided adequate recruits can be supplied under the new conditions.

The possible effects of fishing on a stock of fish may be summarized as follows:

1. Except where only a single age-group is attacked, as in certain salmon, fishing invariably reduces the number of old fish in relation to the number of younger ones.

2. If pursued intensively, fishing may for this reason curtail reproduction beyond the limits of any counteracting forces, and so reduce the species to commercial extinction; particularly where other species are able to maintain themselves, and hence a fishery, in the same habitat.

3. More usually the reduction of large individuals results in a sufficiently increased efficiency of reproduction and (or) of survival of young so that the total stock and production become stabilized, at a level corresponding to the given amount of fishing effort.

4. Other factors compensating for a reduction in stock or favoring an increase in production are: (a) the improved efficiency of utilization of food by a stock consisting largely of young fish, as compared to older ones; (b) possible improved utilization of food by fish which, under the new conditions, may eat more food individually and so be able to divert a larger part of it to growth, less to maintenance.

## OPTIMUM LEVEL OF EXPLOITATION

It is obvious from the above that it may be a complex matter to determine the *best* level of fishing for a given fish population or group of populations. Left to itself, a commercial fishery tends to become stabilized at a level of yield which brings the average rate of wages (or of return on money invested) which prevails in the general economy of the country; or rather, since fishermen are incurable optimists, the usual returns are somewhat less than this. The level of fishing effort so established may or may not be the one which produces the maximum absolute yield, or the best yield taking into consideration the relative market prices of different species, or of one species at different sizes. Populations exploited principally by sport fishermen lack even the profit motive as a regulator, for it is notorious that the effort and expenditure devoted to the capture of a game fish often bears little relation to the value of the catch, considered as an article of food.

Fairly exact computations of the best rate of fishing and the best minimum size, for obtaining maximum yield from a population, can be made from statistics of natural mortality and rate of growth (Ricker 1945), but they cannot ordinarily be projected too far beyond prevailing conditions, because of possible changes in rate of growth or recruitment. Graham's (1935) type of calculation, which attempts to take these latter factors into consideration, unfortunately leans rather heavily on an arbitrary assumption and on a piece of information difficult to obtain. In general both types of calculation will require testing by experiment, but both may serve as useful guideposts.

In a commercial fishery the attainment of the biologically possible sustained yield is of course not necessarily always feasible, because the catch per unit fishing effort may fall below a profitable level before it is achieved. Baranov (1918) has shown that, even in the absence of change in recruitment from year to year, the number of fish caught per unit of effort tends to decrease as effort increases, the rate of decrease becoming very rapid as effort reaches high levels. As there is also a decrease in average age and size of the fish caught, which increased rate of growth will rarely wholly compensate for, it is evident that the limit of profitability of fishing may sometimes be reached before there is any decrease in recruitment, or before the maximum level of sustained yield has been reached. The most extreme expression of this situation is found among fishes whose market value is so small, or which are so difficult to catch, that no fishery for them exists.

On the other hand, decreasing profitability may at times fail to limit expansion of a commercial fishery until the maximum level of sustained yield has been passed, and the same is even more likely to occur in a sport fishery. In that event some lower level of fishing effort would not only produce greater returns per unit effort, but a greater total catch.

Under such circumstances there is a possibility of increasing the catch by decreasing the fishing effort.

In our economy, attempts to increase the yield or the value of fisheries presumed to suffer from over-exploitation have historically taken the form of restrictions on types of gear, fishing places or times, or the size of fish to be taken. More recently a more exact control has been achieved in the Pacific halibut fishery, by setting an annual quota for the catch. Following the limitation of fishing effort by this means, there has been an increase in the availability, the average size, the spawn produced, and hence possibly the rate of recruitment, of this long-lived and late-maturing fish (Thompson & Bell 1934). This method of regulation does not necessarily make for more profitable fishing and certainly puts no effective brake on waste of effort, since an unlimited number of boats is free to join the fleet and compete during the short period that fishing is open. However the stock is protected, and yield approximates to a maximum if quotas are wisely set; as biologists, perhaps we are not required to think any further. Some claim that any mixing into the economics of the matter might prejudice the desirable biological consequences of regulation by quotas (Herrington 1944a).

The State of Maryland has gone one step farther, and may be blazing a trail for the nation to follow whenever reduction of fishing effort is desirable (Tiller 1945). Acting on a plan which is described in detail by Nesbit (1944), they have in effect extended to all coastal fisheries the property rights which have long been recognized in respect to sedentary aquatic resources like oyster beds. The only difference is that each fisherman has an interest in a particular share of the fish stock as a whole, regardless of where it may be found. Starting with the fishermen of 1939 and 1940, the issuing of new licenses has been suspended until fishing effort becomes such as will make for maximum yield. If things work out as with the halibut, fishing at the "optimum" rate should be a very profitable undertaking indeed; and if the licenses were to be made real property, as Nesbit has proposed, their market value would rise to a fantastic figure. Such an abuse would probably bring the whole plan into disrepute; to prevent it the licenses can be made non-transferable and the annual fee charged by the State be made to rise as the profitability of the fishing increases, so that the fishermen would be making a fair income but no more. In this event the benefit of the measure would largely accrue to the state as a whole, while the fishermen's limitation of income would be only a fair equipoise for their having been granted a monopoly of exploitation of a publicly owned resource.

Determining exactly when and where regulations of any of the above types should be imposed is still one of the most important practical questions of fishery biology. While in some situations greater re-

strictions on fishing may seem called for, there are others where it has been shown that existing regulations are unnecessarily severe (Eschmeyer 1945), while for most fisheries data to evaluate the optimum level of fishing do not yet exist.

#### ENVIRONMENTAL ADJUSTMENT

Another approach to greater yield consists in trying directly to improve the *production* in a body of water, in the hope that this will automatically make for more yield. Increase in production may be sought at any trophic level. Considerable increases in primary phytoplankton crops and hence, presumably, in primary production, have been achieved in ponds by adding natural or inorganic fertilizers (Smith & Swingle 1939). By increasing primary production, the production and yield of fish have also been increased, presumably by way of increases at intermediate food levels. Fertilization of large bodies of water is in general not economically feasible, but it often occurs incidentally, as when domestic sewage empties into a lake or stream. In this way tremendous efflorescences of phytoplankton and animal plankton are regularly produced in rivers (Brinley 1942, 1942a). We should expect this to be reflected in production at other trophic levels, up to and including the fishes, but as yet this point has apparently not been critically investigated, on this continent at least.

It may also be possible to increase fish production and yield by obtaining a better percentage conversion of primary plant production to the form of fish. A number of provisional estimates are available of the efficiency of conversion of primary production to fish production: for a small Minnesota lake (Lindeman 1941), for Lake Mendota (Juday 1940), for the Caspian Sea (Bruevich 1939), and so on—all of which are smaller than 1%. Considering this large loss of more than 99% of the energy fixed, it would seem that a relatively small improvement in conversion somewhere along the line could result in a substantial gain in fish production. Unfortunately we know very little about the mechanism by which production is controlled. One might almost say that we know nothing, in comparison with what it would be necessary to know in order to make aquiculture comparable to agriculture. Certainly there seems to be nothing in the waters comparable to the stable balance between producers and consumers such as exists in the grazing of cattle on a well-managed pasture. What is typical in the water is a spectacular plant growth, sometimes followed by or accompanied by a large animal pulse—but with all the irregularity as to intensity and species composition of both, which Pennak (MS) has described. What part is played in this by biotic interactions, and what part by physical factors, is practically unknown.

Under such circumstances we must usually despair of active interference, for the present at least. In the case of plankton, especially, we find that the freshwater species tend to be ubiquitous, so that we

cannot select one or a few algae, say, as the best producers, and keep them alone in a pond. As for the marine habitat, it is mostly a continuous one. An exception is found in certain salt lakes and inland seas, which have become saline in times geologically recent and hence may not have a full complement of marine producers. For example, the diatom *Rhizosolenia* now dominates the phytoplankton of the Caspian Sea, but was introduced there only about 1933 (Zenkevich 1940).

At the level of macroscopic bottom fauna and flora, a certain amount of conscious human intervention can be reported. Owners of trout streams in this country often import *Gammarus*, which somehow has obtained a great reputation as a trout food. The most important effort of this sort however again concerns the Caspian Sea. In addition to species like the bivalve *Mytilaster* or the shrimp *Leander*, which have been taken over accidentally from the Black Sea and have attained enormous abundance, there has recently been a planned introduction of species which are known to be valuable fish foods in the Sea of Azov. The transplantation of the annelid *Nereis* in 1939-40 has now succeeded to the point where these worms have been found in large numbers in sturgeon stomachs (Zenkevich, Birstein & Karpevich 1945). Whether the production or yield of useful fish in the Caspian will actually be increased, it is too soon to know. As regards the larger aquatic plants, various recommendations for introductions have been made in the United States, particularly for new ponds or reservoirs, but no critical investigation of the success or desirability of the introductions appears to have been undertaken. In some situations, vegetation can become so luxuriant that it is a hindrance to yield, and possibly to production as well (Swingle & Smith 1942).

When the trophic level of fish has been reached, man has greater freedom of action. He can, for example, obtain a greater total yield if he uses a plankton-eating fish like the cisco directly, instead of waiting for it to be converted to the form of lake trout. The disadvantage in this is that the plankton-eaters, with some notable exceptions, are usually considered inferior as articles of food; as regards the example just cited, the normal difference in price between cisco and trout would approximately compensate for a loss of 70-80% in conversion. If however the plankton-eating species is rated more highly than are its predators, it may prove worth while to control the numbers of the latter, and so divert some of the production from them to man. This has been done for the valuable young salmon of Cultus Lake on the Pacific coast: the annual *yield* was increased three-fold when their enemies were reduced, without any actual increase in their production (Foerster & Ricker 1941, Ricker & Foerster MS).

Wherever the fish-eating species are considered inferior or worthless, while their prey are esteemed, a good theoretical case can be made out for "predator control." Such species include the gars and bowfin



of the Mississippi Valley states (Lagler, Obrecht & Harry 1942). These species compete with man for their food supply, or compete with more useful fish-eating species. However, any program of control of such fishes is bound to be expensive, and before embarking on one it must be enquired whether the food fishes saved will actually be utilized by man to any considerable extent, directly or indirectly. This is often quite doubtful, because in Indiana at least the rate of exploitation by man of their food species, such as the bluegill, is in general not great; and in any event the abundance of the gars and bowfin is usually not excessive (Ricker 1945a). Another consideration concerns the possible beneficial effect of predation in thinning out the young of desirable fishes. In some lakes overpopulation and stunting is a real danger (Eschmeyer 1938), which piscivorous species may help to avoid.

Another type of management for greater yield consists in the introduction of new species of fishes to a body of water. Fairly often a new species will establish itself in the new habitat. In this way many of our choice American game fishes—trouts, basses, and so on—have greatly extended their ranges, both on this continent and also on the other four. Equally successful has been the spread of the Eurasian brown trout and carp on this continent. (The last-named is much abused by many sportsmen, but wherever it is regularly exploited it appears to be a valuable commercial species.) A fairly recent and widely publicized transfer was of our lake trout to Lake Titicaca in the Andes. From newspaper reports it appears that they have made phenomenal growth in a few years, but that the local fishermen prefer their small native *Orestias*, and fear their catches will suffer because of the competition of the trout.

Whether any of these transfers (except those to formerly fish-free waters) have actually increased fish production has perhaps yet to be proven, but in some instances it is unquestionable that the quality of the fish present has been improved; that is, the newcomers are sought more eagerly than the native species. Much more might be done along these lines, but there is always a danger of liberating undesirable species which might reduce or replace desirable native ones, or of introducing harmful parasites.

#### RELATION OF YIELD TO BASIC NUTRIENTS

In one respect fish which are caught from a body of water differ from the fish which die there. The body substance of the catch is taken away from the basin, and will return only indirectly, if at all. This loss is not to be measured in terms of the basin's yield of fish as compared say with its primary plant production, because in a year's total primary production, as measured on the basis of energy fixed, the same actual atoms (carbon, nitrogen, etc.) may be represented several times over. To illustrate, Bruevich (1939) estimated the annual fish yield of the Caspian Sea as only 0.45% of the annual production of phytoplankton. However, he also estimates the nitrogen in the annual yield to be 2.6% of the

total fixed nitrogen available there, while the phosphorus so removed is about 3.6% of the amount on hand. Doubtless these losses are being made good from the Volga and other rivers, but the example illustrates the fact that a comparison of yield with primary or other productions will not shed light on any possible drain on basic productive resources. The comparison to be made is of the scarcer elements or compounds represented in the yield with the corresponding amounts gained each year from inflow or other sources, less the losses in outflow or in accumulation of unusable stable compounds (chitin, etc.). It is probably such considerations which have influenced some authors to define the "productivity" of a lake solely in terms of the "biogenic" substances present (Ivlev 1945). From this point of view, studies of the "balance" of individual elements or classes of compounds in a body of water may yet have a very practical value. This is true not only of the commonly suspected "minimal" elements, nitrogen and phosphorus, but also of elements required in much smaller quantity (e.g. copper), or even of organic compounds necessary for growth. The already-large literature of this subject cannot be reviewed here.

Whether or not the removal of critical substances in the bodies of the fish caught ever constitutes a factor directly limiting the yield of any natural body of water is not known to the writer. Whether it does or does not, some such substance must set an upper limit to the possibilities of increasing yield by increasing (or decreasing) fishing effort, by introducing new plants or animals as more efficient converters of energy, or by any other method whatever—except fertilization.

#### DISCUSSION

From the analysis of the various investigations cited above, we may ask, what would be involved in a really satisfactory and comprehensive investigation of fish production and yield in a body of water? To reduce the problem to manageable proportions, it would be wise to eschew any attempt at investigating *all* of the fish present, and confine attention to those which play some really significant role in the total economy of the area.

1. In the first place, a quantitative study of the standing crop of both benthic and plankton foods should be made, throughout the whole year. Along with this, estimates of the *production* of the more important benthic animals should be made, using Borutsky's methods or suitable modifications. Attempts should be made to apply similar procedures to the plankton crop.

2. Collections of the important fishes of the area should be made, and their stomach contents determined throughout the year. Feeding experiments in aquaria or enclosures should be designed to give information on rate of digestion, so that, in combination with the observed stomach contents, the daily ration in nature could be determined. Alternatively, Ivlev's method could be used, to determine



the ration directly from wild fish. (A comparison of two methods would be most instructive.)

3. Experiments should be made to determine the percentage of conversion of food to growth in the various fishes, under conditions simulating the natural as regards temperature, daily ration, etc. Some species might refuse to cooperate, but if successful, this plus the observed ration would give the growth and hence the production per fish. Different size-classes of each fish should of course be treated separately.

4. Estimates of the total population of the various common fishes, at different sizes, should be made by the method of direct enumeration, Petersen's mark-and-recapture technique, or whatever else may be suitable. Combined with the previously estimated food consumption per fish, this would give an estimate of the consumption of invertebrate foods, which could be checked against the results obtained by Borutsky's method (1. above).

5. The rate of growth of the fishes should be determined from length frequency polygons or scale markings, and the mortality rate should be estimated from a comparison of successive age-groups or from marking experiments (preferably both), so that a direct estimate of production of each important fish can be made. This will be most accurate if seasonal as well as annual changes in these rates can be determined. This estimate of production should then be checked against the one derived from food consumption plus efficiency of conversion (3, above).

6. Aquarium experiments on rate of growth, efficiency of food conversion, etc., should be tried using rations both greater and less than those observed, as a basis for estimating the probable effects, upon production, of changes in population density. If changes in density or in age-composition of the fish population occur during the time of the study, direct information on possible changes in daily ration, etc. may become available.

7. The yield of fish from the region should be accounted for, including its total weight and its species-, length- and age-composition. From marking experiments or by other means the rate of exploitation should be determined for each important species. From this and the total mortality rate, the natural rate of mortality can be estimated. These data can then be used to forecast the various results of small changes in fishing effort, partly in combination with the results mentioned under 6.

8. Finally, though it is not *directly* involved in fish production, a determination of the plant production in the body of water would be instructive. Much the best methods for estimating phytoplankton production appear to be those involving oxygen formation (Vinberg & Iarovitsina 1939, Riley 1940; also the review by Ivlev 1945); phyto-benthos presents greater difficulties but can be managed (Lindeman 1941). Any attempt to complete a detailed quantitative analysis of the food chains right from plant production to fish production appears to be out of the question as yet; these interrelationships seem almost hopelessly complex—at least in bodies of

water having a flora and fauna normal for these latitudes.

The above may seem an extensive program, and so it is. However it is not necessarily an impossible one, and the importance of the questions involved will make it very worth while for teams of investigators to attack them on a number of bodies of water. Under what were admittedly favorable conditions, many of these items of information were obtained in the Cultus Lake salmon investigation mentioned earlier, and a little extra effort would have yielded some of the others, if their importance had been realized at the time (Ricker & Foerster MS). It seems quite possible that by this time the necessary data may be available for a fairly complete analysis of fish production in such bodies of water as the Barents Sea, the Caspian Sea, the Sea of Azov, or even the North Sea, to judge by the volume of publication concerning these waters before war intervened.

Within the limits of available time it has been impossible to make any really comprehensive search of journals for material which might bear on the various phases of production. Even when known, many references have been omitted, and the selections made may often appear arbitrary. It can only be pleaded that this paper is meant to be, primarily, a review of principles and methods, rather than a compendium of information. It will be justified if it stimulates research and so advances our knowledge of the process of fish production in our waters.

## GLOSSARY

### SCIENTIFIC NAMES OF FISHES MENTIONED IN THE TEXT

- Anchovy—*Engraulis encrasicolus* (Engraulidae)
- Basking shark—*Cetorhinus maximus* (Cetorhinidae)
- Blacknose dace—*Rhinichthys atratulus* (Cyprinidae)
- Blaufelchen—*Coregonus wartmanni* (Salmonidae)
- Bleak—*Alburnus lucidus* (Cyprinidae)
- Bluegill—*Lepomis macrochirus* (Centrarchidae)
- Bowfin—*Amia calva* (Amiidae)
- Bream—*Abramis brama* (Cyprinidae)
- Brook trout—*Salvelinus fontinalis* (Salmonidae)
- Brown trout—*Salmo trutta* (Salmonidae)
- California sardine—*Sardinops caerulea* (Clupeidae)
- Carp—*Cyprinus carpio* (Cyprinidae)
- Caspian shad—*Caspialosa kessleri* (Clupeidae)
- Cisco—*Leucichthys arctedi* (Salmonidae)
- Cod—*Gadus morrhua* (Gadidae)
- Coho salmon—*Oncorhynchus kisutch* (Salmonidae)
- Cut-throat trout—*Salmo clarkii* (Salmonidae)
- Flatfishes—Order Heterosomata (Hippoglossidae, Pleuronectidae, etc.)
- Gars—Lepisosteidae
- Gobies—Gobiidae
- Goldfish—*Carassius auratus* (Cyprinidae)
- Green sunfish—*Lepomis cyanellus* (Centrarchidae)
- Haddock—*Melanogrammus aeglefinus* (Gadidae)
- Halibut—*Hippoglossus hippoglossus* (Hippoglossidae)
- Herring—*Clupea harengus* (Clupeidae)
- Lake trout—*Cristivomer namaycush* (Salmonidae)
- Largemouth bass—*Huro salmoides* (Centrarchidae)
- Long rough dab—*Hippoglossoides platessoides* (Hippoglossidae)

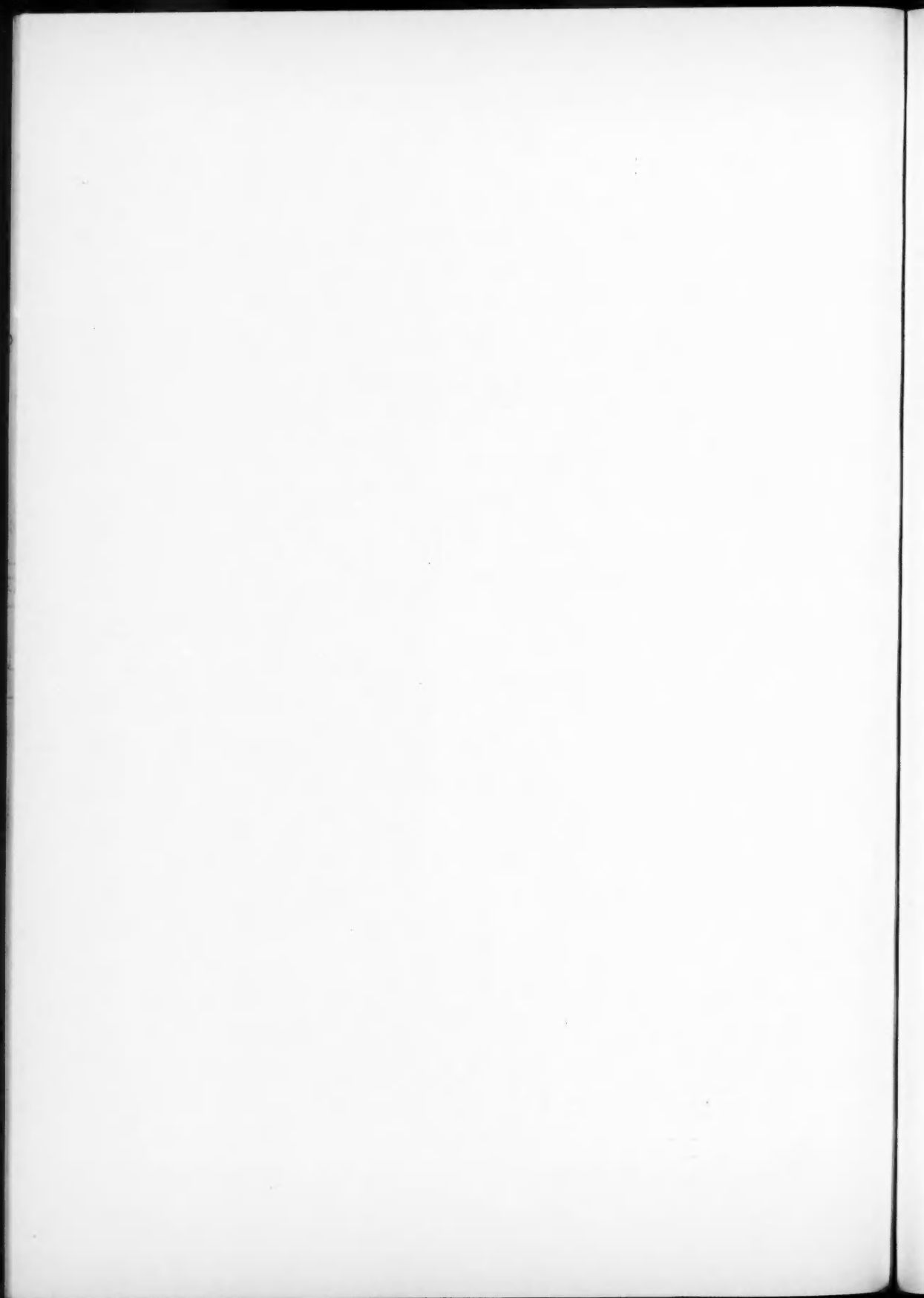
Mackerel—*Scomber scombrus* (Scombridae)  
 Maskinonge—*Esox masquinongy* (Esocidae)  
 Menhaden—*Brevoortia tyrannus* (Clupeidae)  
 Pike—*Esox lucius* (Esocidae)  
 Pilchard—*Sardinops caerulea* (Clupeidae)  
 Pink salmon—*Oncorhynchus gorbuscha* (Salmonidae)  
 Plaice—*Pleuronectes platessa* (Pleuronectidae)  
 Pumpkinseed—*Lepomis gibbosus* (Centrarchidae)  
 Roach—*Rutilus rutilus* (Cyprinidae)  
 Rock bass—*Ambloplites rupestris* (Centrarchidae)  
 Sander—*Stizostedion lucioperca* (Percidae)  
 Sheatfish—*Silurus glanis* (Siluridae)  
 Sockeye salmon—*Oncorhynchus nerka* (Salmonidae)  
 Speckled bullhead—*Ameiurus nebulosus* (Ameiuridae)  
 Speckled trout—*Salvelinus fontinalis* (Salmonidae)  
 Spring salmon—*Oncorhynchus tshawytscha* (Salmonidae)  
 Squawfish—*Ptychocheilus oregonensis* (Cyprinidae)  
 Sturgeon—*Acipenser* sp. (Acipenseridae)  
 Swordfish—*Xiphias gladius* (Xiphiidae)  
 Tiulka—*Clupeonella delicatula* (Clupeidae)  
 Tuna—*Thunnus thynnus* (Thunnidae)  
 Whitefish—*Coregonus clupeaformis* (Salmonidae)  
 Yellow perch—*Perca flavescens* (Percidae)

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A STUDY OF RODENT POPULATIONS ON GUAM,  
MARIANA ISLANDS

LIEUT. ROLLIN H. BAKER H(S)USNR

*Research Division, Bureau of Medicine and Surgery, United States Navy  
Museum of Natural History, University of Kansas, Lawrence, Kansas.*

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## A STUDY OF RODENT POPULATIONS ON GUAM, MARIANA ISLANDS

### INTRODUCTION

During the war period the Laboratory of Mammalogy, U. S. Naval Medical Research Unit No. 2, was engaged in a study of Pacific island mammals in relation to disease. One purpose of the field work was to supply mammals, birds and other animals to the medical research laboratories for examination and experimentation. Another was to preserve specimens for accurate identification. These are deposited in the United States National Museum. A third purpose of the work was to study the mammalian life in order to have at hand information on population densities, habitat requirements, home ranges, breeding periods and other pertinent data, which might be utilized by epidemiology and sanitation units. It was with these purposes in mind that rodent populations on Guam were studied in the period from May to October of 1945.

Three species of rodents are found on Guam: a large rat (*Rattus mindanensis* or a closely allied form of the *Rattus rattus* group), a small rat (*Rattus exulans*), and a mouse (*Mus musculus*). It is interesting to note that the small rats found at Guam are closely related to rats in the New Guinea area which carry chiggers infected with scrub typhus (tsutsugamushi disease) as shown by Kohls *et al.* (1945), and the large ones are related to rats at Leyte (Philippine Islands) which harbor the blood fluke (*Schistosoma japonicum*) as shown by studies of Magath & Mathieson (1945).

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man, who identified plants at the live-trapping study plot, and Glen Lamson, who prepared some of the charts. Lieutenant Commander T. B. Murray, H(S), USNR and Lieutenant Wilfred Crabb, H(S), USNR, then rodent control officers on Guam, supplied field data and specimens on numerous occasions and were in other ways very cooperative.

### HABITATS ON GUAM

Guam (Figure 1) is situated at the southern end of the Mariana Islands at about 13 degrees 30 minutes N. Lat. and 144 degrees 50 minutes E. Long. It is the largest island in the Mariana Chain, being about 27 miles (50 km.) from north to south and has a maximum width of 8 miles (18 km.) from east to west. The area of the island is 225 square miles. The northern part consists of a raised limestone plateau of several elevations with igneous rocks exposed in some localities. The southern part is composed of higher volcanic formations, which on Mt. Lamlam reach the elevation of 1290 feet (570 meters). Scattered limestone deposits occur at various heights in the volcanic area. A well developed system of small rivers drains the volcanic area; most of the flow is to the east. Alluvial soils have been de-



FIG. 1. The island of Guam.

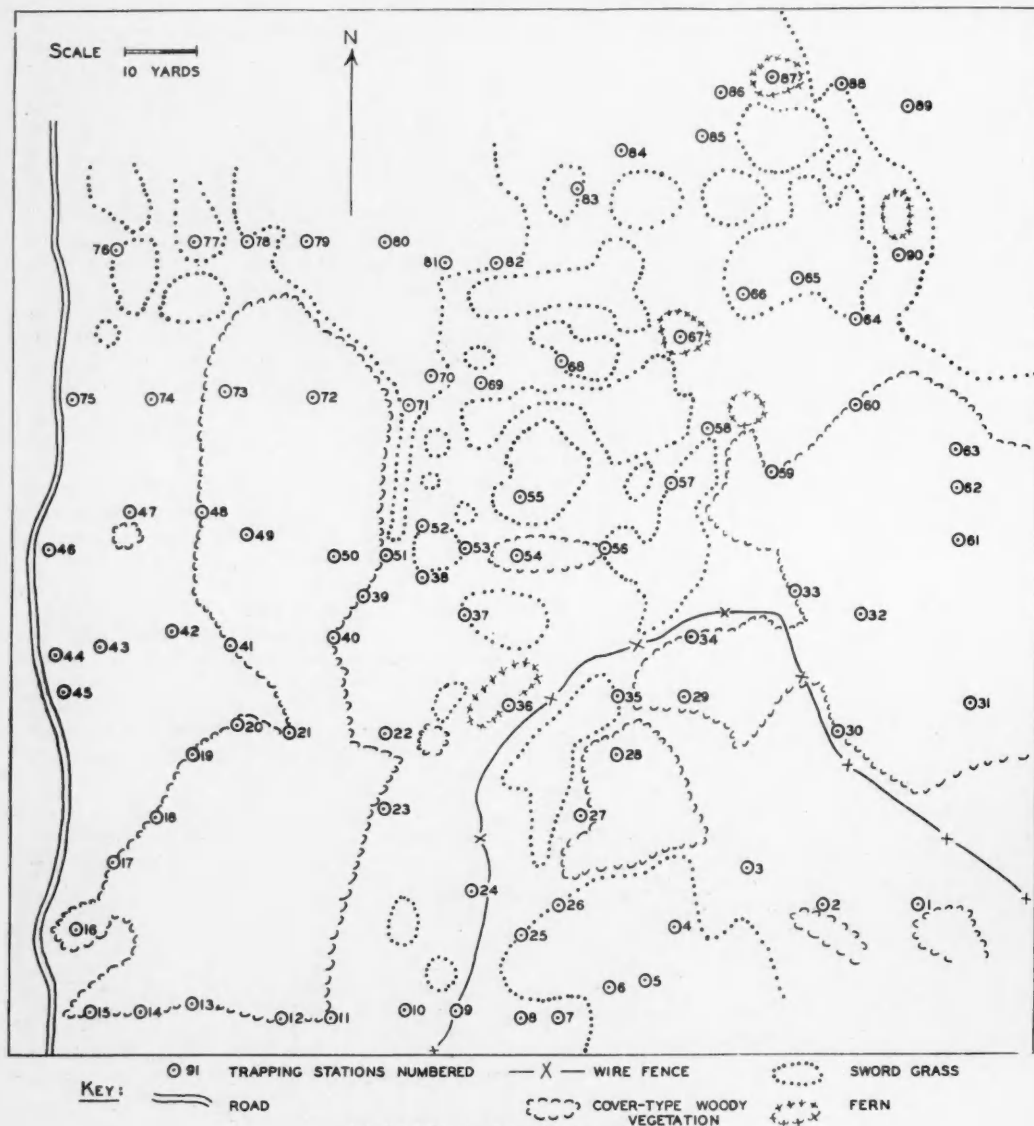


FIG. 2. Santa Rosa Rodent Quadrat.

posited along the rivers and near the beaches. Little surface drainage is present in the northern part, where porous limestone rocks absorb the rainfall. The annual rainfall is approximately 87 inches, much of which falls in the rainy season between May and November. A prominent coral reef is found in many places about the island, especially on the western and southwestern shores. At certain localities, particularly on the eastern side, deep water closely approach the rugged cliffs. Stearns (1937) has written a report on the geology of Guam.

Safford (1905) presented a detailed account of the vegetation of Guam and divided the area into a num-

ber of habitats in regard to the plant associations. Forest, including the coconut groves, and open grassland are the two important environments as far as populations of wild rodents are concerned. The forests usually occur in areas where the soil is derived from limestone. Grasslands and open woodlands are found where volcanic rocks and soils are exposed, except in valleys where the moisture is sufficient to allow for the presence of woodlands.

Forests consist of tall trees and thick undercover of shrubs, vines and ferns. This vegetation is typical of many tropical oceanic islands. Coconuts are grown in cleared forest areas, though as a result

of the war, a thick cover of shrubs and vines now grows in groves that formerly were more open. The grasslands are characterized by sword grass, clumps of which often cover large areas. In the past, the practices of burning and over-cultivating these grasslands have reduced the thickness and the fertility of the soil and have apparently been the causes of the spread of the undesirable sword grass. Burning of grasslands during dry periods for the improvement of livestock grazing has undoubtedly had a deleterious effect on rodents in these areas.

#### STUDY AREA

As a means of studying rodent populations, a trapping program was conducted at a small study plot one mile west of Mt. Santa Rosa in northeastern Guam (Figure 1). The quadrat (Figure 2) measured about 100 yards east to west and about 125 yards north to south and contained 3.1 acres (1.2 hectares). For convenience, quadrat measurements are made in yards and acres. The area was selected because all three species of rodents were present and because grassland, modified forest and coconut grove habitats were included, as shown in Figure 3. The quadrat was situated at the base of the volcanic uplift of Mt. Santa Rosa, and near the junction between the igneous and the limestone rocks.



FIG. 3. Santa Rosa Quadrat: a view along the northern border.

The western part of the quadrat consisted of a poorly drained flat containing a strip of dense grass and weeds, which was joined on the east by a line of small trees and shrubs. Beyond this area the land sloped upward and was covered with herbaceous vegetation and some woody cover, especially at the eastern border. The names of the plants used herein follow Merrill (1914).

Tall grasses (*Paspalum*) and mint weeds (*Hyptis capitata*) dominated the open flats (Figure 4). Other plants were *Cassia*, *Elephantopus*, *Echinochloa*, and *Dryopteris*. Clumps of sword grass (*Miscanthus floridulus*) were found in the northwest corner. A few coconut palms (*Cocos nucifera*) were present



FIG. 4. Santa Rosa Quadrat: a view of the flat area on the western border.

along the southwestern border. The woodland strip contained a number of woody plants including corkwood (*Hibiscus tiliaceus*), screwpines (*Pandanus kahu* and *P. dubius*), orangeberry (*Triphasia trifolia*), and the betelnut palm (*Areca catechu*).

The open hillside plant life (Figure 5) was dominated by an undetermined type of carpet grass together with mint weeds, *Melastoma*, short grasses (*Paspalum*), *Meibomia*, sedges (*Cyperus* and *Fimbristylis*), and ferns (*Lygodium* and *Dryopteris*). Clumps of sword grass were found on the slopes, extensive growths being located on the northern and southern borders.



FIG. 5. Santa Rosa Quadrat: a view of grassy and weedy uplands on the southeastern border.

Woody ground cover was scattered on the upper slopes of the study area, especially in the central portion along the eastern edge. Shrubs and small trees observed include *Morinda*, guava (*Psidium*), inkberry (*Cestrum*), *Clerodendrum*, and *Canarium*. Mint weeds and morning glory (*Ipomoea*) added to the thick nature of the brush. Clumps of bamboo (*Bambusa*) were growing at the southwestern and



west-central boundaries. There are indications that the area had been grazed and that parts of it had been cultivated at some former time. Also, it was evident that fighting between American and Japanese troops took place in the general locality, but there was apparently little destruction to vegetation. The area was well isolated from human habitation, the nearest occupied dwelling being more than one-half mile away.

#### METHODS AND MATERIALS

In May, 90 trapping stations were selected at the quadrat (see Figure 2). Stations were placed at fairly regular intervals through the area, averaging less than ten yards apart. The trap used was the folding Sherman live trap, size 3 x 3 x 9 inches, which proved satisfactory for the capture of all three species of rodents. These live traps were durable, and the majority were utilized, without replacement, throughout the entire trapping period. They proved to be far superior to snap traps for general collecting on Guam and other Pacific islands, except in areas where land crabs were numerous and would disturb the traps.

The bait used was rolled oats mixed with a small amount of ground coconut. It was attractive to the rodents though it was also found that ants and other insects could easily carry it away, and in wet weather it tended to become sticky and clog the trap mechanism.

Rodents were marked and liberated at the stations where captured. One or two toes were removed as a means of identifying individuals. Animals appeared little bothered by this operation. Rodents were shaken from the traps into a cloth sack. The animals were held in the sack with a grip on the head and chest region and were observed and measured without difficulty. Rectal temperatures were taken as part of the examination.

A number of rodents were found dead in the traps. Wet weather and exposure apparently was the cause in most cases, since dead animals were always soaked. Fatalities were most frequent among the mice. *Rattus exulans* appeared the most hardy; none of this species was found dead and none died as a result of handling. Animals exposed to damp conditions within the traps were observed to have spasms before dying. On one occasion a male *Rattus mindanensis* in this condition was brought into the laboratory. After being thoroughly dried with sawdust and warmed a bit, the rat recovered and was liberated the following day at the trapping site. The same rat was later retrapped in the vicinity.

#### LIVE TRAPPING

Trapping was conducted at the Santa Rosa quadrat at five intervals during a total period of six months. It was originally planned that 14-day trapping periods would be alternated with 30-day rest intervals, but other activities prevented strict adherence to this plan. The first trapping period was

for 14 days (May 8 to May 21). After an interval of 30 days, trapping was continued for 10 days (June 21 to June 30). Following another period of 30 days, trapping was again done for 10 days (July 31 to August 9). After 50 days, trapping was continued for 9 days (September 28 to October 6). The final trapping period of 6 days (October 19 to October 24) was begun 13 days after the previous one was completed. During this final period, both live and snap traps were placed at the trap stations in an effort to catch as many of the rodents as possible.

During the first four trapping periods, 172 rodents (69 Mus, 72 *Rattus mindanensis*, and 31 *R. exulans*) were captured. Of these, 150 animals were marked and liberated at the station where taken. The other 22 individuals died in traps or as a result of handling. Eighty-one rodents (25 Mus, 30 *Rattus mindanensis*, and 26 *R. exulans*) were taken in the final kill-trap period; of these 35 were animals marked in former periods.

#### MUS MUSCULUS

##### HABITAT PREFERENCES

Mice were found both in wild environments and in close association with human habitations. There is apparently no recognizable difference between wild and commensal populations. In villages and military establishments, the animals were concentrated where foods were available. After a poisoning campaign at the village of Sinajaña on June 16, Wilfred Crabb collected 28 dead or dying mice in a small area.

Wild-living mice were found in the open grass and brush land which is characteristic of the volcanic parts of the island. They were taken also in coconut groves and other cultivated and fallow areas in the parts of the island where limestone soils are exposed. Mice were not found in the undisturbed jungles.

At the Santa Rosa quadrat, mice were restricted almost entirely to grassy, well-drained uplands, where 96% of the 251 captures were made. In the flat parts of the study area, only 4% of the total catch was taken. Since grassy and brushy areas were found in both the well-drained and the flat parts of the quadrat, it appears that good drainage is an important factor that favors mouse distribution. This was also true where trapping was conducted in other parts of Guam.

##### LIVE TRAPPING

As shown in Table 1, in the first four trapping periods at Santa Rosa quadrat, 53 mice were trapped, marked and liberated, and 24 of these were recaptured in subsequent periods. Figure 6 presents the distribution of marked mice through the trapping periods. The records show that approximately one-half of the animals caught in one period were taken in the immediately succeeding trap period, and that between one-fourth and one-sixth of the animals were taken two periods after initial capture.

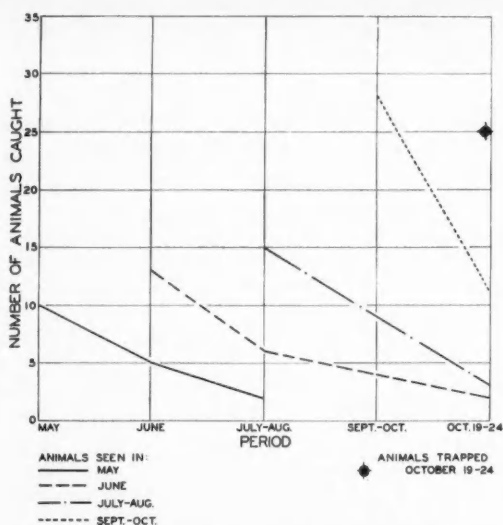


FIG. 6. Distribution of marked *Mus musculus* in the trapping periods at Santa Rosa Quadrat.

An average of 70% of all the mice trapped in each period had not been caught previously. Mice were retrapped more times than other rodents; 53 individuals were taken an average of 3.6 times. Two mice were caught a total of 17 times each, and a number of others were taken 5 or more times.

TABLE 1. Trapping results, *Mus musculus*.

Period	Total catches	New animals	Number marked	Retraps from previous periods	Number retraps within period
May	20	20	10	—	10
June	17	12	9	4	20
July-August	19	12	12	3	35
September-October	34	25	22	6	73
October 19-24	25	14	—	11	—
Total	115	83	53	24	138

Burt (1940), working with *Peromyscus leucopus* in southern Michigan, was able to capture "about all of the mice" in his study area the first two or three nights of live trapping. It will be noted in Table 2 that in the 9-day trapping period at the quadrat in September-October, which was the most successful trapping period of all, some new mice continued to appear throughout the entire interval. The turnover of 70% of the mouse population on each successive trapping period also indicates that new individuals must have been entering the area at a rapid rate.

A number of mice died in traps and as a result of handling. It is probable that some also died after being released, especially those individuals which were recaptured on several successive nights and may have become exhausted or disabled from

trying to escape. Death after release was suspected also by Davis (1945) in working with small rodents in a Brazilian forest.

TABLE 2. Success of trapping *Mus musculus*, September 28 to October 6.

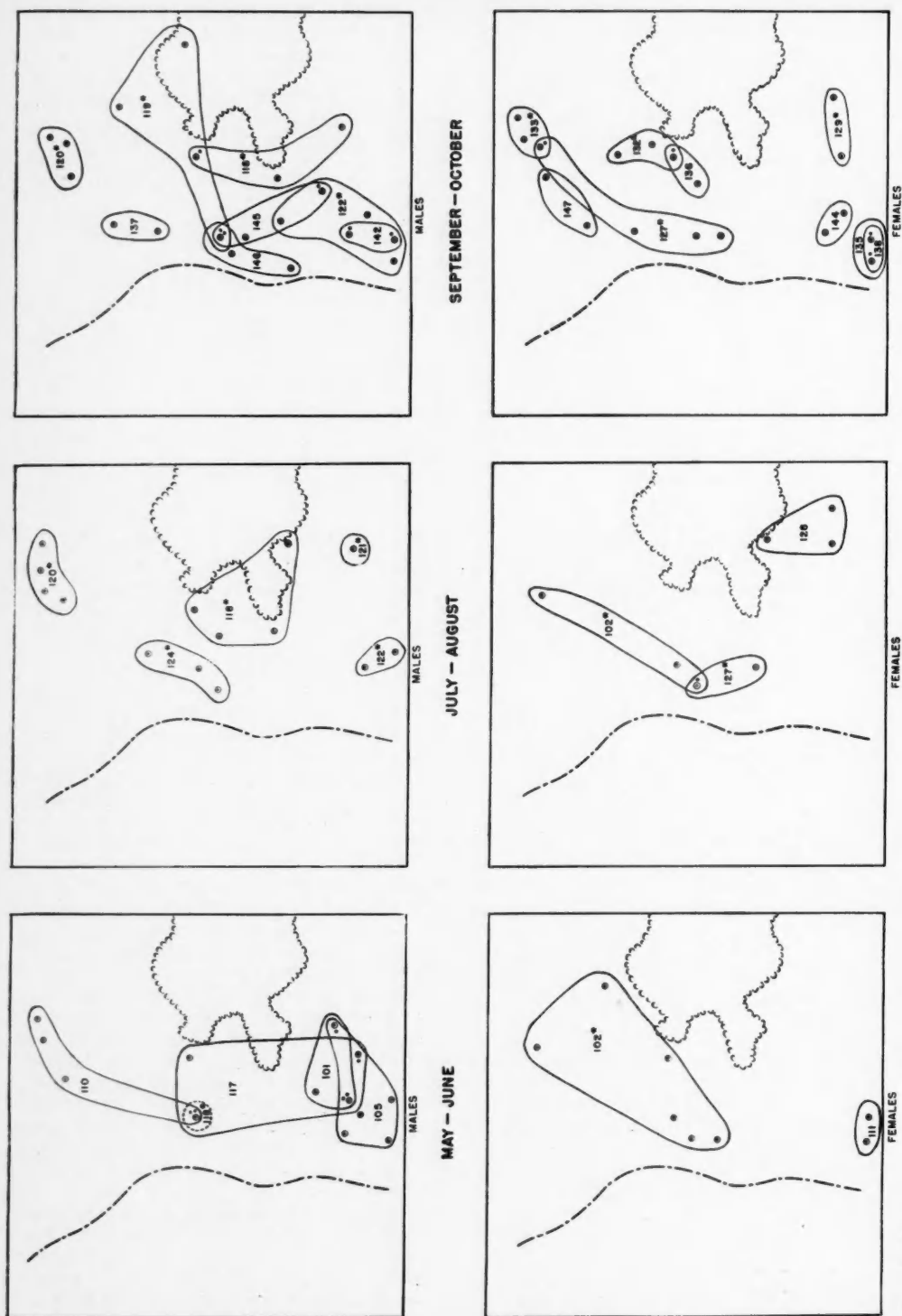
Trapping night	Mice taken	Mice new to this period
First	9	9
Second	11	7
Third	7	2
Fourth	16	5
Fifth	12	2
Sixth	10	1
Seventh	14	2
Eighth	13	4
Ninth	11	2

Burt (1940) rarely recaptured animals if they were not caught in six nights of trapping after once being taken. Similarly, at the Santa Rosa quadrat, of 24 mice recaptured in subsequent trapping periods, only one was retaken after being absent for an intervening period. In contrast, there were 5 such records out of 16 recaptures of *Rattus exulans* and 7 out of 20 of *R. mindanensis*. In the case of mice, at least, it is apparent that when the animals failed to return to trap stations regularly within a particular trapping period they usually were not seen again.

#### INDIVIDUAL RANGES

Movements of mice, as indicated by trap station records, were varied. Records for 169 recaptures show that 38.4% were taken at the same station where previously caught, 41.4% were taken at stations 5 to 25 yards apart, and 20.2% were taken at stations more than 25 yards apart. The mean distance between stations of capture was 14.7 yards. Of 49 animals, excluding those that died in traps before being taken at least three times, 25 were captured three or more times during a single period. The average maximum distance between traps in which these mice were caught within a single period was 29.8 yards for females and 35.8 yards for males. The movements of some of these individuals are shown in Figure 7. The ranges of the males and females are placed on separate maps with each trapping period represented. May and June are treated together because of the small amount of data. Most of the records are for adult individuals. The ranges of females overlapped only slightly but there was more overlap in the ranges of males. Burt (1940) likewise found only slight overlap in the ranges of adult females.

Mice trapped in more than one period appeared to remain in restricted areas. A female mouse, No. 102, was taken in the periods of May, June, and July-August. Its range was quite similar in all these periods. Female No. 127 had a smaller range to the south of No. 102 in July-August. In Sep-



tember-October, however, No. 102 was gone and No. 127 had invaded the area once occupied by the former animal. Female No. 133, first seen in July-August, increased its range slightly in the following period. Female No. 129 shifted its range of movement somewhat from one period to the next. Both of these last mentioned mice were taken at border stations and the extent of their ranges outside the quadrat is not known.

The male mouse, No. 118, was present as a juvenile in a restricted range (one trap station) in June. In July-August its range had increased and also it had moved slightly to the east. In September-October it was still found to maintain about the same range. Nos. 119 and 122 were taken at only a few stations in the early periods, but in September-October they increased their areas of movement considerably. Male No. 120 remained in about the same area for two periods. No. 121 was caught at border stations in June and July-August; the animal undoubtedly ranged beyond the area of the quadrat.

Davis (1945) found small rodents in a Brazilian forest to have a range slightly less than 100 meters in greatest diameter. On the basis of results from live trapping, the mice at Santa Rosa appeared to have ranges of about one-half this diameter.

The results of live trapping indicate that the mice lived in fairly restricted areas. Many animals were found in more than one trapping period, but the majority stayed in limited areas only a short time before they either moved away or were eliminated rapidly by a short life span. Further evidence of a rapid turnover is the fact that when mice were marked and released, at least 50% were retrapped one or more times within that particular period indicating that they were attracted by the traps. However, in the period following when only one-half or less of the marked individuals appeared and new animals were monopolizing the traps, it was apparent that there was a considerable turnover, with old ones gone and new ones taking their places. Davis (1945), working with small rodents in Brazil, recaptured only one-third of the animals after more than one month. He used a line of traps rather than a grid system. Evans (1942), who studied small rodents in England, found that about one-half of his marked animals disappeared one month after capture, and that apparently immigration and emigration were definite factors in population fluctuations.

#### POPULATIONS

The total number of *Mus* captured at the quadrat is presented in Table 3. These figures do not indicate actual populations but may show trends and may be used for comparison with figures for the other rodents. Since mice ranged in the uplands of the quadrat more than in the flatland area, these numbers would be about one-third higher if only the upland is considered. Mice that were found dead in traps within the period first taken are not included in these figures. A low of 3.2 animals to

the acre in May increased to 10.0 in the September-October period. One-third of this peak number consisted of juveniles. The number of young animals increased in the quadrat in the July-August period, with a high point in September-October, and then dropped in the final period.

The total number of mice captured varied from month to month, but these variations possibly are correlated with numbers of the other rodents which occupied much the same type of habitat. This will be discussed later. These figures are comparable with the results of some of the investigations of populations made by workers in the United States. It is obvious here, as in studies elsewhere, that the figures include not only the animals with established territories but also stragglers from adjacent areas and others the ranges of which may include a small part of the quadrat and which only occasionally enter it.

TABLE 3. Number of *Mus musculus* captured per acre at Santa Rosa Quadrat.

Class	May	June	July-August	September-October	October 19-24
Adult females.....	.6	.6	2.0	2.9	3.2
Adult males.....	2.0	3.2	2.6	3.5	4.5
Juvenile females.....	0	0	.6	2.3	0
Juvenile males.....	.6	.3	1.0	1.3	.3
Total.....	3.2	4.1	6.2	10.0	8.0

The presence of such individuals is indicated by the fact that only about one-half of the animals were recaptured three or more times in any one trapping period. As has been stated, however, the calculated ranges of individual mice are small. These small ranges would allow for the presence of a rather large resident population.

#### ACTIVITY

For a given number of traps, more mice were caught at night than in the day. Catches often were better on rainy nights than on other nights. Probably the mice are terrestrial, but I have no evidence that they do not climb trees.

#### HOME SITES

A number of well-used runways were observed on slopes, usually in grassy and weedy areas and often following the drainage pattern. Mice utilized trails of rats and also had smaller ones of their own; at least only mice were taken at stations along some of these small trails. Small burrows were located in well-drained places. A brush pile and a large piece of galvanized iron sheeting at the quadrat were used as protection for nest sites.

#### AGE CLASSES, BREEDING DATA, AND SEX RATIOS

It was difficult to determine the age of captive mice accurately in the field. Very young individuals could be easily distinguished, but the estimation of ages of older animals was less accurate. Measure-

ments taken in the field were helpful. The mice have been divided into two groups, juveniles and adults, on the basis of size, pelage and development of external sexual organs.

As has been shown in Table 3, there was a noticeable increase in the number of juveniles in the quadrat during the trapping periods of July to October. This seems to be correlated with the fact that 4 of 8 adult females in the July-August period were pregnant or exhibited signs of lactation. Trapping in other areas on Guam also indicated that there was at that time a peak in the breeding cycle. Eight of 10 adult females taken at the village of Sinajaña on June 16 were pregnant. Embryos numbered from three to five.

Mice poisoned at Sinajaña on June 16 by Crabb included 15 females and 13 males. Of the 15 females 10 were adults (weights, 10-17 grams) and 5 were juveniles (weights, 7-9 grams). Of the 13 males, 7 were adults (weights, 10-13 grams) and 6 were juveniles (weights, 5-9 grams). This random collection shows 66% of the females and 55% of the males to be adults. Since these mice were taken in and near human habitations, these figures may not apply to wild-living populations.

Of 112 mice taken at the quadrat during the six-month period, 61% were males and 39% were females. The preponderance of males was especially apparent in the mice that were recaptured and in only two periods did the number of females captured equal the number of males. Males were not only retaken more often than females, but more of them were found in two or more periods. Many of the male animals taken only once or twice appeared to be wanderers.

## RATTUS MINDANENSIS

### HABITAT PREFERENCES

*Rattus mindanensis* was the most widespread rodent found on Guam. It was well distributed in the grassy and brushy uplands of the volcanic areas, in the fallow fields and coconut groves, in the rocky coral jungles, and in the villages and around military establishments. In January, 1945, the boxed equipment for the installation of our unit headquarters on Guam was placed at Oca Point in an isolated clearing that was almost surrounded by jungle. It was only a matter of a few weeks before the stock pile became populated with these rats.

At the Santa Rosa quadrat, *Rattus mindanensis* was captured at trap stations in all parts of the area. In the six-month study period, 192 were captured, of which 44% were taken in the 39 stations in the flat, poorly drained portion of the quadrat while 56% were taken in the 51 stations in the upland part of the study plot.

### LIVE TRAPPING

Table 4 presents results of live trapping for *Rattus mindanensis* at the Santa Rosa quadrat. Those rats which were found dead within the first period in which they were taken are excluded. In the first

four trapping periods, 66 rats were marked and released. Of these, 20 animals were recaptured in subsequent periods. Figure 8 shows the distribution of these marked rats through the five trapping periods.

TABLE 4. Trapping results: *Rattus mindanensis*.

Period	Total catches	New animals	Number marked	Retraps from previous periods	Number retraps within period
May.....	37	37	32	..	48
June.....	22	15	15	5	23
July-August.....	13	10	9	2	5
September-October.....	12	10	10	1	3
October 19-24.....	30	18	..	12	..
Total.....	114	90	66	20	79

On the average, 72% of the rats taken in each period was new. Individual animals were recaptured an average of 2.0 times, which is considerably less than the 3.6 figure for *Mus*. The largest number of times that a rat was recaptured was ten. Of all the animals marked and released, only 56% were retaken, while 44% were not seen more than the one time.

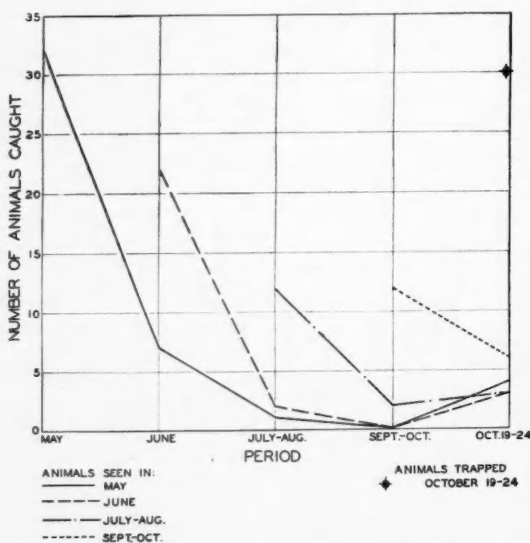


FIG. 8. Distribution of marked *Rattus mindanensis* in the trapping periods at Santa Rosa Quadrat.

Live trapping for *Rattus mindanensis* appeared to be more effective than for *Mus* (compare Tables 2 and 5). Most of the rats new to the period were taken in the first half of the operation.

Only a few rats died from handling or trapping. As in the case of *Mus*, however, it is quite likely that some rats died after being released. Several of them were liberated in a rather weak state.



TABLE 5. Success of trapping *Rattus mindanensis*, May 8 to 21.

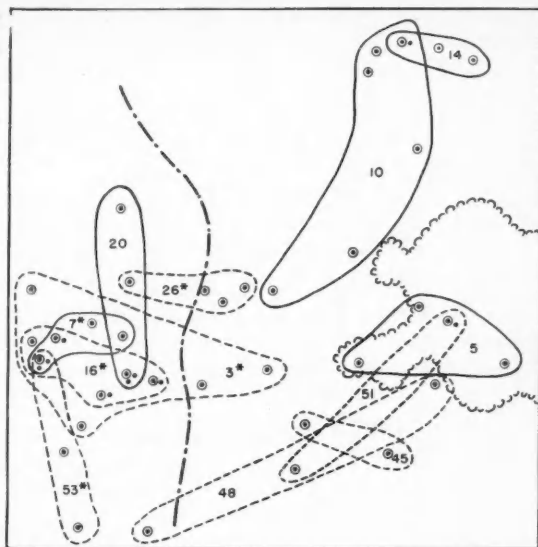
Trapping night	Animals taken	Animals new to this period
First.....	13	13
Second.....	8	4
Third.....	6	4
Fourth.....	8	3
Fifth.....	8	2
Sixth.....	9	2
Seventh.....	10	3
Eighth.....	5	1
Ninth.....	3	1
Tenth.....	4	0
Eleventh.....	2	0
Twelfth.....	2	0
Thirteenth.....	2	2
Fourteenth.....	4	1

## INDIVIDUAL RANGES

Of 102 recapture records, 24.5% were for animals taken at the same station, 47.1% were for rats taken at stations 5 to 25 yards apart, and 28.4% were for rats taken at stations more than 25 yards apart. The average distance between catches was 17.0 yards.

Owing to the small number of records for some of the trapping periods, only the combined results for May and June are plotted. These ranges are shown in Figure 9. For rats taken three or more times within a single period, the average distance between points where these animals were taken was 26.6 yards for females and 37.3 yards for males. Many of the ranges bordered the edges of the quadrat so it is likely that some of the animals ranged beyond the limits of the quadrat. The north-western corner of the quadrat was apparently little used by rodents. There were few captures in this area; runways and other evidences of rodent activity were lacking. There was considerable overlap in the ranges of male rats but the ranges of females more often were separated. The ranges of the females were restricted to the upland area, which may indicate their preference for well-drained locations for breeding sites.

As in the case of *Mus*, the resident *Rattus mindanensis* appeared to live in restricted localities, but it was quite apparent that the individuals in the area changed frequently, since only one-third of the marked rats returned in later periods, and a 72% turnover was found in each subsequent period. However, some of the males, recaptured only a few times in several periods, might have ranged in a larger area and entered the quadrat only occasionally. Four males were taken in May and retrapped as late as the final October period. No. 26 was captured six times, at five different stations, in May, June and October; the maximum distance between stations was 39 yards. The stations included no border ones, all being well within the boundaries. No. 16 was trapped 8 times in May, June, and October at six stations



MALES

MAY - JUNE



FEMALES

Scale 0 10 20  
yards

- \* Taken in other trapping periods
- Denotes adult animal
- - - Denotes immature animal
- - - - Division between flatland and upland
- ~~~~~ Woody upland

FIG. 9. Movements of marked *Rattus mindanensis* in the periods, May and June, at Santa Rosa Quadrat.

on the western border, where it moved at least 32 yards. No. 7 was taken six times in May and October at five stations on the western border, where it ranged for 31 yards. No. 27 was taken twice, in May and October, at one station on the eastern border. Probably the last three rats lived outside of the study plot part of the time.

#### POPULATIONS

Table 6 presents the total number of *Rattus mindanensis* obtained from the live trapping. Animals known to have died within the period concerned are not included. A high of 11.6 animals per acre in May dropped to 4.2 in September-October and increased again to 9.3 in late October. The number of juveniles varied from a high of 60% in July-August to a low of 6% in October.

TABLE 6. Number of *Rattus mindanensis* captured per acre at Santa Rosa Quadrat.

Class	May	June	July-August	September-October	October 19-24
Adult females.....	3.2	1.9	1.0	1.6	4.2
Adult males.....	4.8	2.6	1.0	1.6	4.5
Juvenile females.....	1.3	1.0	1.3	0	.3
Juvenile males.....	2.3	1.6	1.6	1.0	.3
Total.....	11.6	7.1	4.9	4.2	9.3

These fluctuations in the trapped numbers of *Rattus mindanensis* from period to period were not very different from those found for the mouse population. In May there was a high population of rats recorded at the quadrat. Of 37 individuals caught at this time, 17 were recaptured two or more times in the 14-day operation. In June most of these rats had disappeared and fewer new ones were encountered. The number of rats taken in the third and fourth periods was small. These low figures may be partially explained by the wet conditions which prevailed during these particular trapping operations. The flat area of the quadrat was often covered with water. There was a high number seen again in late October, with a recovery of 16 marked animals from every previous period (Fig. 8).

#### ACTIVITY

Rats were occasionally seen in the daytime on Guam in woodland and grassy areas and even in trees. Some were captured during daylight hours, especially about supply dumps. *Rattus mindanensis* was found to be a good climber, and it is likely that these rodents spend considerable time in trees.

#### HOME SITES

Rats made homes in burrows, in trash and brush piles, in fallen logs, in tree hollows, and in clumps of tree ferns. Wharton studied nests of these rats in his work on ectoparasites and will discuss the subject in a paper to be published by him. Rats fed on a variety of vegetable matter at the quadrat and often piled food materials near their homes. One pile of partly eaten pandanus fruit parts was found

at the study plot under a clump of sword grass, at least 25 yards from the nearest pandanus tree.

#### AGE CLASSES, BREEDING DATA, AND SEX RATIOS

At the quadrat, as shown in Table 6, juveniles included between 24 and 37% of the population, except in the July-August period when a high of 60% was found and in the final October period when only 6% of the total population was juvenal. In the field examinations, subadults were classed with adults; therefore the actual breeding population may be a lower figure than the one given.

At and near the village of Agat on May 16, a random collection of *Rattus mindanensis* taken by Wilfred Crabb following a poisoning campaign numbered 157 individuals. Of these, 95 were females including 37 adults (weights, 106-185 grams), 24 subadults (weights, 50-101 grams) and 34 juveniles (weights, 15-48 grams). This age classification was based on weights, measurements, character of the pelage, and degree of development of the sex organs. Of the 37 adult females, 13 were pregnant. The number of embryos varied from 4 to 8. Of the 62 males collected, 14 were adults (weights, 114-160 grams), 17 were subadults (weights, 50-112 grams), and 31 were juveniles (weights, 17-43 grams). This population of only 35% adult females and 24% adult males appears to indicate that a peak in the birth of young had just occurred. As in the case of the mice taken at the village of Sinajaña, the population figures here may not apply to wild-living animal communities.

Of 116 rats taken at the Santa Rosa quadrat during the study period, 58% were males and 42% were females. Here, as was found in the mouse population, there was a larger number of males. Males were also recaptured more times than females and retrapped in the quadrat over a longer period of time.

#### BODY TEMPERATURES

Temperatures of captured animals were taken in the field by the use of a mercurial thermometer in the rectum. A summary of the data is presented in Table 7. Temperatures of males averaged 35.5° C., and females averaged 36.4° C. A male near death from exposure in a trap had a temperature of 33.5° C. In a summation of studies on the body

TABLE 7. Rectal temperatures of *Rattus mindanensis*.

Sex	Number of animals	Number times temperature taken	Mean temperature	Minimum	Maximum
Males.....	30	67	35.5°C	32.8°	38.3°
Females.....	18	35	36.4°	33.1°	39.4°

temperature of the laboratory rat, Donaldson (1924) concludes that the animal does not regulate its body temperature very well, and that environmental temperatures may cause fluctuations. This seems to account for the variation in temperatures of the trapped *Rattus mindanensis*, since the temperature

within the trap could vary considerably. The higher temperature of females is in accord with Donaldson's findings. The average temperature of these rats is slightly lower than those of laboratory animals studied by him.

### RATTUS EXULANS

#### HABITAT PREFERENCES

*Rattus exulans* appeared to have the most restricted distribution of the rodents at Guam. It was found in the grassy and brushy uplands, where volcanic soils are exposed, and also in coconut groves and fallow fields. Like the mouse, it was not found in undisturbed coral jungle, but unlike both the mouse and *Rattus mindanensis* it was rarely taken within villages. The population appeared spotty, as trapping results indicated. At some localities *Rattus exulans* was numerous, at other places the population appeared small and often was overshadowed by a larger number of *Rattus mindanensis*.

At Santa Rosa quadrat, *Rattus exulans* was distributed in all parts of the plot, but appeared to prefer the well-drained uplands. Of 88 captures, 74% were taken in upland type while 26% were found in the flat part.

#### LIVE TRAPPING

Table 8 shows the catch of *Rattus exulans* at the quadrat and Figure 10 presents the distribution of marked animals through the trapping period. Thirty-one animals were marked and liberated in the first four periods, of which 17 were recaptured in subsequent periods. New rats each period totaled 69% of the catch. Animals were recaptured an average of 2.2 times. Of 31 rats marked and released, 24 were recaptured at least once while seven individuals were taken three or more times in any one period.

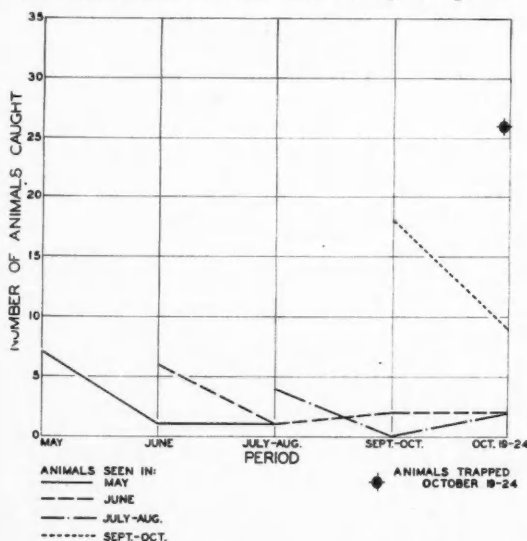


Fig. 10. Distribution of marked *Rattus exulans* in the trapping periods at Santa Rosa Quadrat.

These retrapping figures are higher than those of the other two rodents. The greatest number of times a rat was taken was six. No *Rattus exulans* died as a result of trapping or handling. The animals appeared to withstand the live trapping better than did either of the other two species.

Using figures for the most successful trapping period, September 28-October 6, Table 9 shows that the live traps were effective in catching most of the *Rattus exulans* within the first half of the operation.

TABLE 8. Trapping results, *Rattus exulans*.

Period	Total catches	New animals	Number marked	Retraps from previous periods	Number retraps within period
May.....	7	7	7	..	6
June.....	7	6	6	1	5
July-August.....	4	2	2	2	1
September-October.....	18	16	16	2	16
October 19-24.....	26	14	..	12	..
Total.....	62	45	31	17	28

TABLE 9. Success of trapping *Rattus exulans*, September 28 to October 6.

Trapping night	Animals taken	Animals new to this period
First.....	3	3
Second.....	4	4
Third.....	2	2
Fourth.....	3	1
Fifth.....	6	4
Sixth.....	3	2
Seventh.....	3	1
Eighth.....	4	0
Ninth.....	6	1

#### INDIVIDUAL RANGES

Of 45 recapture records for *Rattus exulans*, 22.2% were taken at the same station, 55.3% were taken at stations 5 to 25 yards apart and 24.5% were taken at stations more than 25 yards apart. The average distance between catches was 17.4 yards, which is very similar to the average distance for *Rattus mindanensis*. In Figure 11 the ranges of male rats taken in the period of September-October are plotted. For male rats taken three or more times in one period, the average distance between traps in which these animals were taken was 41.0 yards. There is not sufficient data with which to plot ranges of females. Rats Nos. 79 and 83 were taken at stations within the quadrat. Nos. 77, 81, and 97 were taken at border stations and probably ranged beyond the limits of the area.

Of 31 *Rattus exulans* marked and released, 24 were recaptured at least one time, suggesting that the animals tended to remain in one locality. However, the appearance of an average of 69% of new ani-

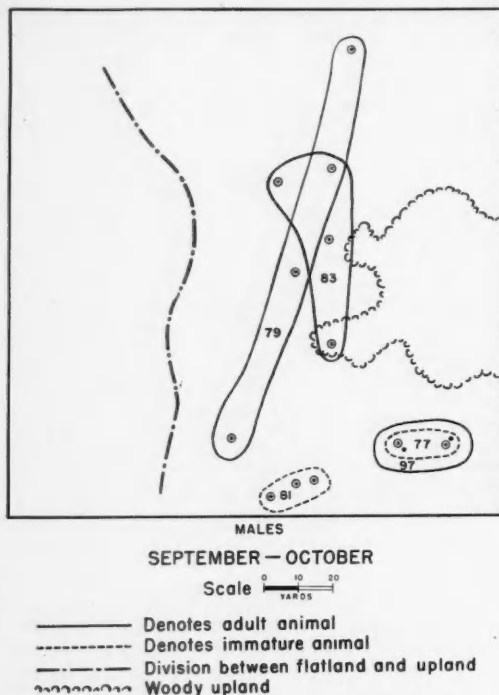


FIG. 11. Movements of marked, male *Rattus exulans* in the period, September-October, at Santa Rosa Quadrat.

mals in each period indicates a turnover corresponding closely to that of the other species of rodents. The fact that almost one-half of the rats seen in September-October were also taken in the final period further indicates that the activity of these animals was confined to small areas. The fact that several animals were taken over a period of three or four months (Fig. 10) also indicates a long residence in one locality. However, as in the case of *Rattus mindanensis* some of the males may have ranged over areas larger than the quadrat and returned to the trap stations only occasionally. It is also possible that the study quadrat may have been at the edge of a population concentration of this species and the writer's observations may have been influenced by the "spilling-over" effect of such a population.

#### POPULATIONS

Table 10 presents the trapped population of *Rattus exulans* at the quadrat. In May 2.5 animals per acre were found. This number dropped to 1.2 in the July-August period and increased to 5.8 and 8.4 in September-October and late October respectively. The number of juveniles (13.3%) was quite low, especially in comparison with juveniles of the other rodents.

*Rattus exulans* populations reacted much like those of *R. mindanensis*. In the early periods of trapping few animals were taken or retrapped, but in Sep-

TABLE 10. Number of *Rattus exulans* captured per acre at Santa Rosa Quadrat.

Class	May	June	July-August	September-October	October 19-24
Adult females.....	.6	1.0	.3	1.0	2.6
Adult males.....	1.0	.6	.3	4.2	5.8
Juvenile females.....	.3	0	.3	0	0
Juvenile males.....	.6	.6	.3	.6	0
Total.....	2.5	2.2	1.2	5.8	8.4

tember-October the number of individuals greatly increased.

#### ACTIVITY

*Rattus exulans* was active in daylight hours. There was no evidence that this animal climbed trees as did *Rattus mindanensis*.

*Rattus exulans* appeared to be a much more aggressive animal than *Rattus mindanensis*. On one occasion a *Rattus exulans* was placed in a cage with several of the larger *Rattus mindanensis*. Almost immediately the smaller animal began fighting the larger ones and succeeded in blinding two of them before it was removed.

#### HOME SITES AND FOODS

*Rattus exulans* ranged along the same runways used by the other rodents. All three species were taken at the same stations placed along such trails. The rats used burrows and surface nests in debris and piles of coconut husks.

Stomachs of six *Rattus exulans* contained about one-fifth insects and other invertebrate animal parts and about four-fifths vegetable matter.

#### AGE CLASSES, BREEDING DATA, AND SEX RATIOS

*Rattus exulans* had the smallest percentage of juveniles of any of the rodents. Three adult females taken in May and June exhibited signs of pregnancy or lactation, but no extremely young rats were seen. Most of the males observed had testes descended.

Of 60 *Rattus exulans* taken at the quadrat, 72% were males and 28% were females. This unbalanced sex ratio offered further evidence that this particular area might have been at the edge of a concentrated population of this species, and the "spilling-over" effect might have caused this apparently abnormal sex ratio.

#### BODY TEMPERATURES

Table 11 presents rectal temperatures of *Rattus exulans*. These temperatures are similar to those

TABLE 11. Rectal temperatures of *Rattus exulans*.

Sex	Number of animals	Number times temperature taken	Mean temperature	Minimum	Maximum
Males.....	5	7	35.5°C	34.2°	37.1°
Females.....	4	9	36.4°	34.4°	37.9°

obtained for *Rattus mindanensis*. It may be noted that the temperature of the female (36.4° C.) is also higher than that of the male (35.5° C.), as in the case of the other species of rat.

## RODENT POPULATIONS

### DENSITY

Table 12 presents the total number of animals taken at the quadrat in the study period. The trapped population varied between 12.3 and 19.0 animals per acre in the first four trapping periods, with a high of 25.7 in the final kill-trap period of October 19-24. These figures are for the quadrat as a whole. In the upland area, which comprised about two-thirds of the quadrat, a higher population was found, since *Mus* and *Rattus exulans* were trapped more often in this habitat. As has been stated, this trapped population included the actual resident animals as well as a certain number of transients, juveniles, stragglers from adjacent areas and others the home ranges of which may have included a small part of the quadrat. The method employed by Stickel (1946) in calculating the actual resident population cannot be successfully used for this small area. The number of animals taken in the first four periods of live trapping was probably more indicative of the actual population than the number taken in the final period when snap traps were used. The number of adult females captured was between one-third and one-fourth of the total catch.

TABLE 12. Number of rodents captured per acre at Santa Rosa Quadrat. Adult females are in parentheses; other figures represent both males and females.

Species	May	June	July-August	September-October	October 19-24
<i>Mus musculus</i> .....	3.2 (0.6)	4.1 (0.6)	6.2 (2.0)	10.0 (2.9)	8.0 (3.2)
<i>Rattus mindanensis</i> ...	11.6 (3.2)	7.1 (1.9)	4.9 (1.0)	4.2 (1.6)	9.3 (4.2)
<i>Rattus exulans</i> .....	2.5 (0.6)	2.2 (1.0)	1.2 (0.3)	5.8 (1.0)	8.4 (2.6)
Totals.....	17.3 (4.4)	13.4 (3.5)	12.3 (3.3)	19.0 (5.5)	27.7 (10.0)

The high point found in the final six-day period seems logical because snap traps should be more effective in capturing the animals. The removal of animals and the resulting release of population pressure probably allowed a number of rodents from adjacent areas to enter and be caught. A catch of 81 rodents was made, all but 6 animals being taken in the first four nights.

### RODENT INTERRELATIONSHIPS

Where the three rodents were found together on Guam, they seemed to occupy the same ranges and eat the same kinds of foods. This was apparent at the study quadrat. There was no indication of the extent of tolerance between the species although it appeared that there was competition for food and home sites, especially between the two species of rats. The only evidence of possible friction between the animals at the area was the finding of a partly

eaten *Rattus mindanensis* in a snap trap in late October. Blair (1943), who studied small mammals in New Mexico, found no evidence of competition between the species living together in a small area. Within the species, the females appeared much less tolerant of other females than the males did of other males.

The density of a rodent population is, of course, dependent on the amount of food, cover, den sites, predator pressure and other factors that regulate the carrying capacity. At Santa Rosa quadrat, the trapping results indicated that there was a rather stable population during the six-month study period, although there was a drop in numbers during the summer months.

Although these variations in the total population from period to period are evident, it is apparent also from Table 12 that more drastic fluctuations occurred within the individual species. Especially in the early periods, there was some indication that the population of one species fluctuated in relation to others, and that the ratio of one species to another varied in order to maintain a carrying capacity population.

### MOVEMENT OF RODENTS

The protected part of the home range, that which is referred to as the individual's "territory" by Burt (1943), was not evident. Probably the animals have certain private areas, possibly immediately adjacent to home sites.

Apparently, males of both *Rattus mindanensis* and *R. exulans* often ranged over areas larger than the quadrat; at any rate one-third of these rats that were recaptured in a later period were not taken in one or more intervening periods of trapping. The 50-day interval between the third and fourth trapping periods did not seem to cause any appreciable loss in marked animals when the results were compared with those where shorter rest periods intervened. Blair (1943), trapping small rodents in New Mexico, found that the wood mouse (*Peromyscus leucopus tornillo*) was nomadic and remained in one range only a short time before moving. Some of the individuals at Santa Rosa quadrat appeared to behave in a similar manner.

Experience derived from this study indicates that the area where animal populations are to be studied should be as large as can be adequately observed. Although the area utilized here was apparently larger than the individual home range of any animal present, a quadrat five acres or more in size probably would have given more significant results. It would have also been interesting to have placed a large number of traps entirely around the quadrat during the final kill-trap period to determine how far away some of the marked animals had moved. This was contemplated at the time, but other work prevented setting the traps.

### RELATIONSHIPS TO OTHER ANIMALS

There appeared to be few natural predatory enemies of rodents on Guam. Hawks and owls are only



occasional visitors to the island, and wild carnivores are absent. Domestic cats apparently are well established in the wild environments. A feral cat, shot at the quadrat in May, was found to have rat bones and hair in its stomach. Dogs were not encountered far from human habitation and are probably not an important enemy of the rodents. The large monitor lizard (*Varanus indicus*) may prey on rodents although no evidence was obtained concerning the matter. The crow (*Corvus kubaryi*) and the egret (*Egretta intermedia*) are two birds which may be enemies of the rats. I have no evidence that the coconut crab and other large land crabs prey on rodents, although they will molest trapped animals.

The introduced toad (*Bufo*) was abundant at the quadrat. Toads were either attracted by the bait and the insects which were found in the traps or used the traps as resting places, since the toads were troublesome during trapping operations. Land, hermit and robber crabs were rare in the area. Snails and slugs often sprung the traps. Ants and roaches ate and carried away the bait.

Mites and lice were frequently observed on rodents at the quadrat. A large tick (*Amblyomma*) was occasionally picked up on clothing but was not found on any of the animals observed at the area.

#### SUMMARY

As a means of studying the life habits of rodents on the island of Guam, Mariana Islands, a live trapping program was conducted at a study quadrat in the period from May to October, 1945. The quadrat contained 3.1 acres and was situated about one mile west of Mt. Santa Rosa. Ninety stations were selected at the area as permanent live trapping locations. Rodents were captured, toe-clipped, and liberated in four trapping periods: May 8 to May 21, June 21 to June 30, July 31 to August 9, and September 28 to October 6. During the fifth period, October 19 to October 24, snap traps were utilized.

One hundred and seventy-two rodents of three species, *Mus musculus*, *Rattus mindanensis*, and *Rattus exulans*, were captured in the first four periods. Of these, 150 were marked and liberated at the stations where taken. Forty percent of the marked animals were recaptured in two or more trapping periods. Eighty-one rodents were taken in the final snap trap period.

Trapping records indicate that the rodents lived in small ranges of less than one acre in area. However, it was apparent that the individual rodents did not remain in these ranges for long periods, since about 70% of the trapped population each subsequent period was new. A considerable portion of this moving population was thought to be transients and juveniles and not the actual resident animals.

It seemed evident that some of the males of *Rattus mindanensis* and *R. exulans* ranged over areas larger than the quadrat, as shown by their infrequent captures over a period of several months. This appears to indicate that the animals were out of the quadrat and returned occasionally.

Information regarding habitat preferences, density, home sites, age classes, weights, relationships to other animals, and other data are presented.

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CYCLOMORPHOSIS IN *DAPHNIA*

I. An Analysis of *D. retrocurva* and *D. galeata*

JOHN LANGDON BROOKS

*Osborn Zoological Laboratory, Yale University  
New Haven, Conn.*

A dissertation presented to the Faculty of the Graduate School of Yale University in partial fulfillment  
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## CYCLOMORPHOSIS IN *DAPHNIA*

### I. An Analysis of *D. retrocurva* and *D. galeata*

#### INTRODUCTION

Cyclomorphosis can be defined as cyclic form change in a series of genetically identical generations. It is known to occur in species of fresh-water dinoflagellates, rotifers and cladocerans. All of these reproduce by asexual or parthenogenetic processes. Many members of the genus *Daphnia* which inhabit the open portion of all but the smallest bodies of fresh-water exhibit striking seasonal form changes. Some of these are the subject of this investigation.

It is a pleasure to express my gratitude to two persons among the many who have offered their help during the course of this investigation. Prof. G. Evelyn Hutchinson has unstintingly offered invaluable advice, aid and criticism from the time when he first interested me in this problem, until the manuscript was completed. This close association has been a constant source of inspiration. My wife has not only provided the moral support which was much needed at times, but also aided me in innumerable ways, particularly on field trips and in the preparation of the manuscript.

#### A CRITICAL REVIEW OF LITERATURE ON CYCLOMORPHOSIS IN *DAPHNIA*

##### *Information from Observation and Correlation with Environmental Variables*

The study of this phenomenon of cyclomorphosis began in the closing years of the last century and has since been sporadically pursued by various biologists. Coker published a general review of cyclomorphosis in *Daphnia* in 1939. As this is the case the present review of the literature will cover only the main developments which are antecedent to the investigation herein reported. This previous work has followed either of two lines. One consists in observations of the sequence of events in a cyclomorphic population and an attempt to correlate these events with environmental variables. The other was the experimental approach. In none were the two methods combined.

The name of C. Wesenberg-Lund will always be associated with cyclomorphosis. His pioneer work, primarily that published in 1908, revealed the general features of the seasonal form changes of all the groups of fresh-water species found in Danish lakes. The main results of these painstaking researches, inasmuch as they concern cyclomorphosis in *Daphnia*, are summarized in the following statements.

1. Most of the planktonic *Daphnia* undergo more or less extreme seasonal variation.

2. Seasonal variation of all forms begins in all of the Danish lakes at the same time, "proceeds suddenly, so to speak by abrupt transitions, being completed on the whole in 2-3 weeks." (p. 246).

3. This sudden onset of variation occurs when the water temperature is at 14°-16° C.

4. At this temperature, the young *Daphnia* are born with longer helmets than their mothers had at birth. After birth these helmets grow much more than those of their mothers.

5. Temperature is assumed to be the cause of this variation.

In 1923 Wagler studied populations of *Daphnia cucullata* from 110 localities in Europe. He attempted to correlate the body size and helmet size of each population with the physical characters of the body of water in which it was found. His Plate 14 contains a camera lucida drawing of an average primiparous female, taken during midsummer, from each of 87 populations while his Table 18 gives the name of the body of water where each was collected, the surface area and maximum depth, if known, and the date of the sample.

As the conclusions which Wagler reached contradict both of the two main currents of thought on cyclomorphosis, it is considered important that the validity of his conclusion be checked. To do this a graphic representation of the relation between size of habitat and body size of *D. cucullata* seemed desirable. Surface area (given in Wagler's Table 18) is used as an index of the size of the body of water. This is plotted against the number indicating the position of the *Daphnia* in the size seriation (Wagler's Plate 14). The logarithm of the area is used in order to compress the scale. The resulting scatter diagram is given as Figure 1, for those 54 populations that inhabited lakes of known area. The area for the Frederiksborg Castle Lake was taken from Berg & Nygaard (1929). Three ponds (Nos. 6, 7, 11) are less than one hectare in area, but are plotted as 1 hectare. The tendency for the smallest forms of *D. cucullata* to occur in the smallest ponds and larger ones in larger lakes is undeniable. However, Wagler's statement of the relationship does not seem justified. This particular relationship between body size and size of habitat holds only for *cucullata* as demonstrated. It is the opposite of the relation between species of the genus *Daphnia*. For these it is in general true that tycho planktonic species are larger than the limnoplanktonic ones.

"Bei der Betrachtung der primiparenreihe der Tafel 14 stellt es sich heraus, dass der Anordnung der Tiere

eine bestimmte Gruppierung der Fundorte entspricht: die kleinen Rassen sind in den kleinen und flachen Teichen zu Hause, die grösseren in mittleren Teichen und kleinen Seen, und die Riesen sind vorwiegend Bewohner tiefer und grosser Seen der baltischen Platte (vgl. Tabelle 18). Kleine Ausnahmen bestätigen die Regel nur, niemals ist aber zu verzeichnen, dass eine der grossen Formen in einem Kleingewässer auftritt und dass eine kleine Rasse das Limnetikum eines grossen und tiefen See bevölkert." (Wagler 1923, p. 295.)

That part of this statement relating to the giant forms seems particularly suspect. Of the fourteen (one fourth of the total number plotted) largest forms entered in the diagram, one half are easily within the size range of the lakes supporting medium sized *cucullata*. The maximum depths of these fourteen are indicated on the diagram along with the depths for other lakes of the same area. Wagler's conclusion that the largest forms are found predominantly in lakes deeper than those in which the medium sized forms occur seems to be no more accurate than his statement relating to area.

Wagler's assertion concerning the relation between helmet size and body size is open to still graver criticism.

Die höchsten Köpfe besitzen die Riesenrassen, mittelhohe die mittलगrossen, und rundköpfig sind die kleinen Varianten. (p. 298.)

Although this is apparently based upon a study of the drawings of his Plate 14, a glance at these shows that the largest forms do not have helmets of the greatest relative size. Absolute helmet size is rather meaningless depending as it does on the total size of the animal. It cannot be used as an index of the development of cyclomorphosis. Measurements of the drawings show that in fourteen forms the head length is equal to or greater than the carapace length. Ten of these can be plotted. The other four are undoubtedly small lakes as the morphometric data are wanting. The positions of these four populations in the size seriation are indicated by arrows on the baseline. The distribution of the symbols representing these ten populations on the diagram (Fig. 1) makes it evident that the largest forms do not possess the relatively highest helmets and do not occur in the largest lakes. The only legitimate statement that can be made is that the smallest forms, in the smallest bodies of water, are roundheaded. No elaborate statistical treatment is needed to indicate that, except for such small roundheaded forms, the distribution of the various head shapes and sizes is a random one.

Wagler, however, draws the conclusion that the forms with the highest helmets occur in the larger and deeper lakes. Since large and deep lakes are cooler in summer and have less nutritive material available than do small, shallow ponds in which roundheaded forms occur, he further concludes that high temperature and good nutrition prevent the formation of helmets. This final conclusion based as it is upon inaccurate generalizations and assumptions is completely worthless. It is of importance

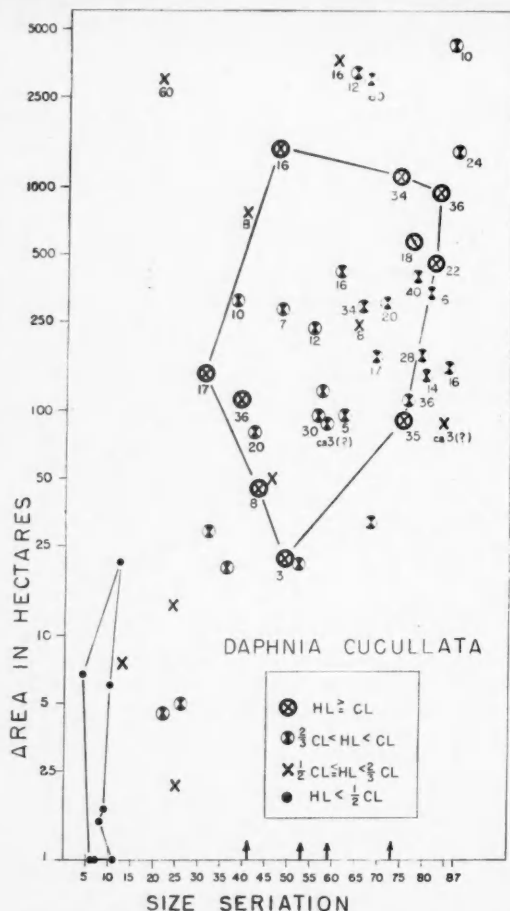


FIG. 1. This scatter diagram showing the relation between body size in *D. cucullata* and area of habitat, is based upon data presented in Wagler's (1923) Table 18 and Plate 14. This relation is indicated for the 54 bodies of water for which records of area are available. Envelopes enclose the points representing the populations with the relatively smallest and the relatively largest helmets. The numbers which are found below some points give, in meters, the maximum depth of the lake. The areas are plotted on a logarithmic scale. The arrows indicate the position of the four lakes whose *D. cucullata* belong to the class with the relatively tallest helmets, but for which morphometric data are wanting.

that the invalidity of Wagler's conclusion be shown, as it contradicts both of the main hypotheses on the environmental determination of cyclomorphosis, namely the Wesenberg-Lund-Ostwald contention that helmets develop at higher temperatures, and Woltereck's assertion that a high level of nutrition is the most important factor in helmet formation.

The contribution of Hsi-Ming (1942) is the only one from the Woltereck group to furnish any new information of importance through the analysis of seasonal change as it occurs in lakes. He gives the



seasonal variations of carapace length and relative head length for seven populations of *Daphnia* found in five subalpine lakes of southern Germany. Six of these are *Daphnia longispina* which show minimal variation and are of a type previously considered non-cyclomorphic. The sixth belongs to *D. cucullata* and has a tall helmet during the summer.

The most significant result of this work is the undeniable proof which it furnishes that the relative head length of these *Daphnia longispina* with low round crests undergoes cyclic variation following the same pattern seen in forms which reach more spectacular proportions. It is also clear that the absolute carapace length in the *longispina* populations changes during the course of the year, although the amplitude is very small. This material which afforded an excellent opportunity for morphogenetic analysis, was unfortunately devoted as were most of the researches of Woltereck's students, to an attempted disproof of the Wesenberg-Lund-Ostwald buoyance theory of the adaptive significance of cyclomorphosis. Because of the manner in which Hsi-Ming has recorded his results it is difficult to gather much information concerning the seasonal variation in the relative growth rates of the head.

#### INFORMATION DERIVED FROM EXPERIMENTAL STUDIES

Ostwald (1904), Woltereck (1908-1928) and Coker & Addlestone (1938) have endeavored through the use of experiments, to determine the factors affecting head size in *Daphnia*. Unfortunately they have reached contradictory conclusions, with Ostwald and Coker & Addlestone on one side, Woltereck on the other. Both Ostwald and Woltereck used *D. cucullata* as experimental animals. Woltereck used *D. longispina* for some of his earliest work but turned to *cucullata* with which it apparently was easier to work. Ostwald's specimens came from lakes in the vicinity of Plön, primarily Schöe-See, while Woltereck indicates that most of his results were obtained by using animals derived from the Frederiksborg Castle Lake population (Hilleröd, Denmark). It is exceedingly improbable that the differences in their conclusions can be attributed to genetic differences between the two groups of animals. Coker & Addlestone worked on *Daphnia galeata* which is very different from the large-helmeted *cucullata*, as it has at most a small angulate helmet. This population came from University Lake, Chapel Hill, North Carolina. Woltereck's results will be discussed first, then those of Ostwald and Coker & Addlestone.

Woltereck states that there are two factors which control helmet formation. One is the nutrition of the mother; the other is the generation number. He contends that the only way in which temperature plays a part is by altering the rate of food uptake by the mother. He claims that neonatae hatched from ephippia are always roundheaded and that the adults into which these develop always lack the helmet even under the best nutritive conditions. The neonatae of the sixth parthenogenetic generation, under the same conditions, have tall helmets nearly

as long as the carapace and develop into adults with tall helmets. His measurements (1921, p. 110-111) indicate that in all cases mature females have relatively shorter helmets than they had as neonatae. However, the helmets of sixth generation adults reared under good conditions were very tall. Those of the first generation were very low, and those of poorly fed sixth generation individuals were but slightly taller.

As experimental work, the researches of Woltereck are most unsatisfactory. It is exceedingly difficult to derive any clear picture of what he did, or of what his results really were, as opposed to what he thought they should have been. All of the papers giving the above information, with the exception of the 1921 paper which is a summary, are very sketchy and designated by Woltereck as preliminary reports, to be followed by detailed accounts. In not one case has the promised full report materialized. This makes appraisal of this work impossible. One can only say that Woltereck claims to have done experiments which indicate that nutrition and generation number are the two prime variables determining the size of the helmet.

At this point mention must be made of two experiments done by Berg (1936) which tested Woltereck's assertion that generation number plays a role in helmet formation. Berg hatched ephippia and reared the first generation females thus obtained at 22° C. with plenty of food. Although the heads of the neonatae completely lacked helmets, the second and subsequent instars were helmeted. This contradicts Woltereck's contention that the adult ex-ephippion females lack helmets though reared at high temperatures with abundant food. Both men used *D. cucullata* from the Frederiksborg Castle Lake. It is regrettable that Berg does not give the temperature at which the ephippia were hatched. These experiments indicate that generation number does not have the influence over postembryonic helmet growth which Woltereck states. No one has ever found any confirmation of the "Woltereck" effect of generation number.

The experimental findings of Ostwald offer a great contrast to those of Woltereck. These were published in 1904, four years before Woltereck's first report on *Daphnia*. Adults of *D. cucullata* were brought into the laboratory in the fall. Those with the tallest helmets were kept at 0-5° C., and those with shorter helmets kept at about 20° C. The sizes of the heads of the neonatae produced at the different temperatures are recorded as drawings, said to have been made with a camera lucida. The figures are rather grotesque and display little knowledge of the anatomy of the animals. Nevertheless they clearly indicate that the heads of neonatae born at 20° C. are much larger than those born at 0-5° C. These offspring suffered, as did their mothers, from malnutrition and they died within a few days. Ostwald's experiments, although crude, did show that even with very poor nutrition tall helmets were produced at high temperatures, low helmets at low tempera-

tures. What is more he showed, by transferring two females with broods of different ages from one temperature to another, that temperature acts during the middle period of embryonic development.

The experiments of Coker & Addlestone (1938) are by far the most satisfactory. They worked, however, on a form with a low degree of form change. In numerous experiments they found that the neonatae reared below 11° C. are roundheaded while those reared about 15° C. always have pointed, so-called "spike," heads. At intermediate temperatures both round and spike-heads occur with the percentage of the latter increasing at 15° C. is approached. The size of the spike increases above 15° C. being quite prominent on neonatae reared at 20° C. A series of transfer experiments showed that temperature is ineffective after a certain stage in development (the time of appearance of the two nauplius eyes) has been reached. This confirms Ostwald's suggestion based upon his meagre data. They found no evidence that generation number affects the development of the spike on the neonate head. A very important observation was that this spike, present in neonatae reared above 15° C., was lost after the first few molts.

#### AIMS OF THE PRESENT INVESTIGATION

It will be clear from the preceding discussion that the problem of the causes of cyclomorphosis has yet to be solved. Several hitherto unexplored possibilities for investigation are evident.

Although this problem is largely one of relative growth it has never been attacked as such. Nor is it possible to gain any knowledge of relative growth by examination of the data of Wesenberg-Lund and Hsi-Ming. These are both deficient in three ways.

1. None of the series of samples were begun at the beginning of the season, but always in the middle (June-July). As each season is slightly different from the next, interpretation of the exact sequence of events in the development of cyclomorphosis in these cases is impossible.

2. The samples are separated by too long intervals. Most of the animals present in a given sample must have died before the next collection was made, making relative growth analysis difficult.

3. Insufficient morphometric information is presented to permit fruitful analysis. Although Wesenberg-Lund has apparently made very numerous measurements, the number published is inadequate. Hsi-Ming's results are given in graphic form of such a type that reworking the data is most uncertain.

Therefore, it was apparent that a series of samples should be made at a locality with a strongly cyclomorphic *Daphnia*. The series should begin early in the spring while temperature is still low. The interval between samples should be relatively short, viz. about two weeks. Adequate numbers must be taken at each sample. This material can then be subjected to a relative growth analysis. A record of concomitant physical factors should be made, per-

mitting study of the correlation of these factors with the cycle of morphological changes.

In none of the previous investigations has the experimental work been correlated with a study of the natural cycle of the same population. Therefore, experiments on the influence of temperature and nutrition should be performed on a strongly cyclomorphic *Daphnia* which is at the same time being studied in the lake. Of the more detailed previous experiments, those of Coker & Addlestone on the mildly cyclomorphic *Daphnia galeata* alone seemed a significant point of departure. It is, however, obviously desirable to confirm and if possible to extend their findings.

#### A NOTE ON TAXONOMY

It has become evident during the course of this investigation that each of the two types of *Daphnia* discussed below constitutes a separate biological entity. In accord with this view each will be considered as constituting a species. The form with the retrocurve helmet, widely distributed through the north-central and northeastern parts of the United States and southern Canada, is clearly the *Daphnia retrocurva* of S. A. Forbes, 1882. The form which develops an angulate, spiked head during certain times of the year is referred to the species *galeata* as defined by G. O. Sars in 1863. Sars published no figure at that time and many forms with both acutely and bluntly angulate heads have been placed in this species. It is impossible at the present time to state the relationship of these forms (as described by Sars, P. E. Müller, Richard, etc.) to the forms for which the specific name *galeata* is here used. The known American distribution of *Daphnia galeata*, as the species is here conceived, is the Eastern United States. It is common in ponds and lakes in Connecticut (Bantam Lake, Highland Lake, Lake Compounce, Lake Shenipsit, Mt. Tom Pond). The *Daphnia* from University Lake, Chapel Hill, North Carolina, which has been studied by Coker & Addlestone (1938) is of this species. Banta (1939) figured spike-headed *Daphnia* from two localities, Lake Okechobee, Florida, and a pond near Cold Spring Harbor, Long Island. These both belong to *D. galeata*.

A thorough taxonomic treatment of the genus *Daphnia*, with particular reference to the North American continent, is being initiated. The author would greatly appreciate material from any part of the world. It should be sent to the Osborn Zoological Laboratory, Yale University, New Haven, Conn., U. S. A.

#### ANALYSIS OF CYCLOMORPHOSIS IN *DAPHNIA RETROCURVA* IN NATURE

##### RELATIVE GROWTH ANALYSIS

##### *Collection and Selection of Material*

As Bantam Lake contains a population of limnetic *Daphnia* which develops helmets larger than any other known from Connecticut, it was chosen as the best site for further investigation. This lake, which

has been described by Deevey (1940), has an area of 405.4 hectares (ca. 1000 acres) making it the largest natural body of water in the state. The maximum depth is 7.3 meters; the mean depth 4.4 meters. The great areal extent of the lake together with its small mean depth prevents the development of persistent thermal stratification in summer. This is advantageous in the present research as this lack of stratification reduces the number of environmental variables to be considered. The lake occupies three basins of which the central one is largest in surface area and has the largest mass of water of maximum depth. A bathymetric map is included in the Supplement to Bulletin No. 63 Conn. State Geological and Natural History Survey. Vertical series of plankton samples were taken near the center of this deepest area. These samples were taken with a Foerst-Juday plankton trap of 10 liter capacity at each meter down to 6 and sometimes at 7 or 7.5 meters if the water level was high. The depth was measured to the top of the trap. As the mass of water cut off by this sampler is 26 cm. deep, the specimens collected were from the 30 cm. below the depth indicated. Sampling in this manner permitted a study of the vertical distribution and ensured the inclusion of all parts of the population regardless of the vertical distribution. Two catches were made at each depth one from each side of the rowboat to eliminate errors due to supradispersion. As the same volume of water was sampled on each date, population size and density can be readily compared. The plankton catch was preserved in a 5% formalin solution.

Surface and bottom temperatures were taken with a reversing thermometer. Some midsummer readings at 3 meters were also taken. An adequate supply of oxygen was present at all depths in this mesotrophic lake which mixed completely in midsummer when there was a strong wind. These samples were made at two-week intervals from April 1 to August 10, 1945.

#### Methods of Measurement and Analysis

The plankton samples were examined and counted with a binocular dissecting microscope. A record of vertical distribution was kept and the specimens which had been preserved without distortion were set aside for measurement. Four races of *Daphnia* were present during 1945; one is referable to *D. galeata*, one to *D. retrocurva*, two to *D. longispina*. From the accompanying table (Table 1), it is evident that the *D. retrocurva* population was present throughout the period in sufficient numbers to promise a fruitful analysis. About 100 of the best preserved specimens from each series were used in the morphogenetic analysis, the first two series being supplemented by vertical plankton net hauls. The August 10 catch with the races most differentiated was examined first, and last the early spring samples when there was greater need for discrimination of little differentiated forms.

The measurements made differ from those of previous investigators. The body is conceived as being

TABLE 1. Sizes of populations of 4 races of *Daphnia* in Bantam Lake, 1945. The figures given are the total numbers of animals in the vertical series of plankton trap catches. The total volume of water sampled on each date is 160 liters.

Date	<i>retrocurva</i>	<i>galeata</i>	<i>longispina</i> "rounderest"	<i>longispina</i> "apicate"
April 1.....	3	34	0	0
" 15.....	75	25	0	0
" 29.....	3333	340	12	0
May 13.....	5127	680	8	0
" 27.....	3905	285	9	0
June 14.....	4406	181	91	13
" 28.....	935	6	160	18
July 9.....	474	10	393	45
" 21.....	188	0	58	83
Aug. 10.....	183	0	77	36

composed of two morphological units whose relative rates of growth we wish to study: the head, and the carapace. Reference points must be chosen which bear the same morphological relations throughout development. In measuring the carapace length, CL, the anterior extension is a concise landmark, but the posterior termination is not. In the early instars the posterior extension of the carapace is well defined (Fig. 2). In the later instars, due to more rapid growth on the dorsal side at the base of the tail spine, this reference point is no longer the posteriormost part of the carapace, but appears to be the inflection point in the gentle S-curve of the postero-ventral margin of the carapace. The distance between these points, on a line parallel to the long axis of the carapace, is CL. (Fig. 2.) Carapace width, CW, is the greatest distance between dorsal and ventral margins of the valves, at right angles to their long axis. This dimension, which is not defined by fixed points throughout development, is of value chiefly as a check against errors in the measurement of CL. Head width, HW, is the greatest distance, normal to the long axis of the carapace, between the dorsal and ventral margins at the base of the head. (Fig. 2.) The tail spine was measured from the point of juncture of the outer and inner chitinous layers comprising the carapace. These measurements (HW, TS) will not be considered in the following discussion.

The measurement of the head with the retrocurve helmet presents a more difficult problem than did any of the other entities. Measurement along the extended long axis of the carapace is obviously inadequate, and the diagonal from the tip of the helmet to the midpoint of the base of the head also becomes more inadequate as the curvature increases. The unsuitability of these straight lines as indices of head length is apparent in Figure 2. The length of the ventral margin is a measure of the maximum growth, that of the dorsal a measure of minimum growth. A helmet will be of the retrocurve form only when this is the case. There must obviously be a line between the two whose length is an index of the average growth. A curved line midway between the two margins will be an approximation to

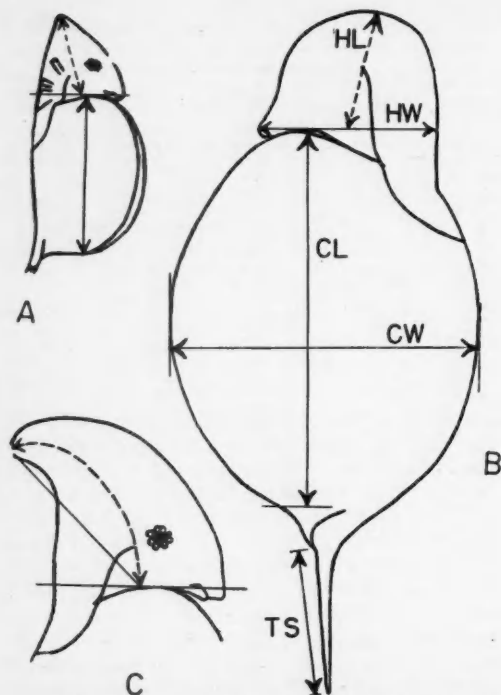


FIG. 2. Camera lucida drawings of *Daphnia retrocurva* showing measurements. The double-headed arrows indicate, on a round-headed adult from an early spring sample (B), the five measurements made. The method of measuring the CL on a young specimen is shown on a neonata (A). It is to be noted that the length of a helmet of this size is closely approximated by a straight line (pecked). However, the length of a large helmet of an adult of midsummer (C) cannot be measured by a similar straight line (solid). The length of the curved midline (pecked) is taken as the HL of such specimens.

the required mean. It should be emphasized that this mean line is a measure of the average growth rate of the head, hence it is not comparable to the length of the midline of an uncurved helmet which is an index of maximum growth. The chief objection to using the anterior margin as an index of growth is its inappropriateness in the round-headed forms of spring. The apex of the helmet determines the anterior end of the midline, while the posterior end is the midpoint of the base of the head (Fig. 2).

To measure the length of this curved midline it is necessary to make camera lucida tracings of the head. The midline is drawn in by sight and checked by drawing perpendiculars along its length, making certain that the line passed through the midpoints of these perpendicular segments. With well developed helmets the position of the midline is obvious; with the lowest ones the place on the rounded margin comparable to the apex of pointed forms is sometimes more difficult to determine exactly. However, the differences due to variations in placing the apical point are small. The length of the curved

line is then measured with a rotameter reading in mm.

In the following pages the chief method of analysis consists in the study of relative growth; it is therefore of importance to ascertain whether any of the conclusions arrived at might be artifacts due to substitution of projections for dimensions of the actual growing surfaces, the hypodermis. In the usual procedure of measurement the specimens are arranged on their sides in water, with the aid of the dissecting microscope, in a plane as nearly perpendicular to the line of vision as possible. The lengths measured either by ocular micrometer or on camera lucida drawings are the lengths of the projection of curved surfaces upon a plane. To gain some conception of the length of the curved hypodermis camera lucida tracings were made of representative specimens of different sizes and degrees of helmet development, as seen from the ventral surface. The length of the curved outline of the carapace, in the focal plane showing maximum curvature, provides a close approximation to the actual length of the hypodermal fold which comprises the valve of the carapace. The length of the outline at the appropriate focal levels approximates the actual length of the hypodermis of the head measured along the curved line midway between dorsal and ventral margins. The results are presented in Table 2. The curved outline of the carapace is from 1.10-1.19 times the length projected on the median plane. That of the head is 1.04 to 1.10 times the standard HL measurement. More important is the relation which the ratio

$\left\{ \frac{\text{hypodermal length}}{\text{projection length}} \right\}$  for the head bears to that of

the carapace for different instars. This relation is expressed by the numbers in the last column. All of these values are less than one, which means that in all these cases the curved length of the head hypodermis is never as much greater than its projection as the curved length of carapace hypodermis is greater than its projection. In the specimens (B, C) with large helmets, the value is closest to unity, indicating that the relative length of the hypodermis of the head is only slightly less than the standard measurements (projections) indicate. The relative hypodermal head length of the small helmeted specimen (D) however, is much less than appears from a measurement of projections. Therefore, there must actually be a relatively faster growth of the head, in order to change the value from 0.910 to 0.973, which is unsuspected from a study of the lengths of the projections only. It therefore appears that if measurements of the curved growing surfaces had been practical the results obtained would have been even more striking than those set out below, because the value of  $k$ , the relative growth exponent, is clearly a little too small when derived from projection measurements of individuals with high helmets. To epitomize this discussion we may say that the difference, that will be apparent between isauxetic growth and tachyauetic growth is even greater than that indicated in the subsequent analysis.



TABLE 2. *Daphnia retrocurva*. Relation of length of curved hypodermal surfaces to length of projection of these onto a plane. All measurements in micra.

	I Hypodermal length (Length of outline)	II Projection length (Length of median line)	I II	Head Carapace
Carapace.....	1350	1138	1.19	0.925
Specimen A (April 28)				
Head..... (round)	445	402	1.10	
Carapace.....	981	883	1.10	.973
Specimen B (July 21)				
Head..... (helmeted)	729	682	1.07	
Carapace.....	871	782	1.11	.964
Specimen C (July 21)				
Head..... (helmeted)	610	569	1.07	
Carapace.....	835	729	1.145	.910
Specimen D (July 21)				
Head..... (helmeted)	495	475	1.04	

An indication of the measuring errors is presented in Table 3. When the ocular micrometer was used to measure an object with definite reference points (2) the measuring error was small. The measurement of largest carapaces (1) introduces two other sources of error. One is involved in resetting the scale when the object is longer than the micrometer; the other, more serious, in choosing the inflection point in the gentle curve of the postero-ventral carapace margin. The percentile deviation is now three times as great, about 3.5%. Although all specimens were oriented as nearly as possible in a plane parallel to the focal plane some variation is introduced here. An attempt to measure this variation was made in series (3) and (4). The specimen of the previous two series was used, being reoriented between measurements with the aid of the dissecting scope in the usual manner. In (3) a fixed point was taken as posterior end of CL, and the variation is small. For shorter lengths the error was about 2%. In the third set, the extent of the error involved in measuring the head length was examined by means of camera lucida tracings. In series (5) one of the five measurements was deliberately made with the specimen oriented at a much greater angle to the focal plane than was permitted in the course of the investigation. This value was 663 as compared with a mean of 687.5 micra from four good measurements (5a). In (5b) this low value is included in the calculation. Series (6) deals with a small helmet, less than one half of the size of that in (5). The percentile deviation is about twice as great, viz. 2%. The greatest error—3.5% appears to be involved in the measurement of large carapaces where a subjective element enters. The measurement

of small objects with the ocular micrometer entailed a slightly greater error than did the method of measuring head length, where the percentile deviation was not more than 2%.

TABLE 3. *Daphnia retrocurva*. Estimation of errors involved in different procedures of measurement.

Method	Mean Length in Micra	Number Measured	Standard deviation	Percentile deviation = stand. dev. mean length
Ocular micrometer, specimen in same position	(1) CL 1123	5	39.10	3.48
	(2) HL 393	5	4.24	1.08
Ocular micrometer specimen re-oriented between measurements	(3) CL 1128	5	9.45	0.84
	(4) HL 386	5	8.82	2.29
Cam. luc. tracing; draw. curved midline;	(5a) HL 687.5	4	6.95	1.01
Meas. midline with rotometer	(5b) HL 682.6	5	11.60	1.70
	(6) HL 300.8	5	5.88	1.95

As Julian Huxley (1932) indicated, the growth of an organ or part of a body often proceeds at a rate which, relative to that of the rest of the body, may remain constant over a considerable period of development. This growth relation can be expressed

$$y = bx^k$$

where  $y$  = dimension of a part, and

$x$  = corresponding dimension of whole body or another part.

Exponent  $k$  is the index of the relative growth rate; when  $k = 1$ , the part grows at same rate as whole (isauaxisis);

$k > 1$ , part is growing faster than whole (tachyauaxisis);

$k < 1$ , growth is less than that of whole (bradyauaxisis).<sup>1</sup>

The constant  $b$  is the value of  $y$  when  $x = 1$ .

When the values of  $x$  and  $y$  are plotted on a double logarithmic grid, they will fall along a straight line if  $k$  is constant.

$$\log y = k \log x + \log b$$

is the form of the equation of a straight line, and

$$k = \frac{d \log y}{d \log x} = \text{slope of the line.}$$

In the problem at hand, we are interested in the rate at which the head is growing with respect to the rest of the body. The size of the head is represented by value HL. CL is taken as the most accurate index of the size of the body of a *Daphnia* with which the size of the head should be compared. A plot of these points on a double log. grid gives a clear picture of the relationship between these values at any time in the population (Fig. 3).

<sup>1</sup> The terms in parentheses are those recommended by Needham (1942).



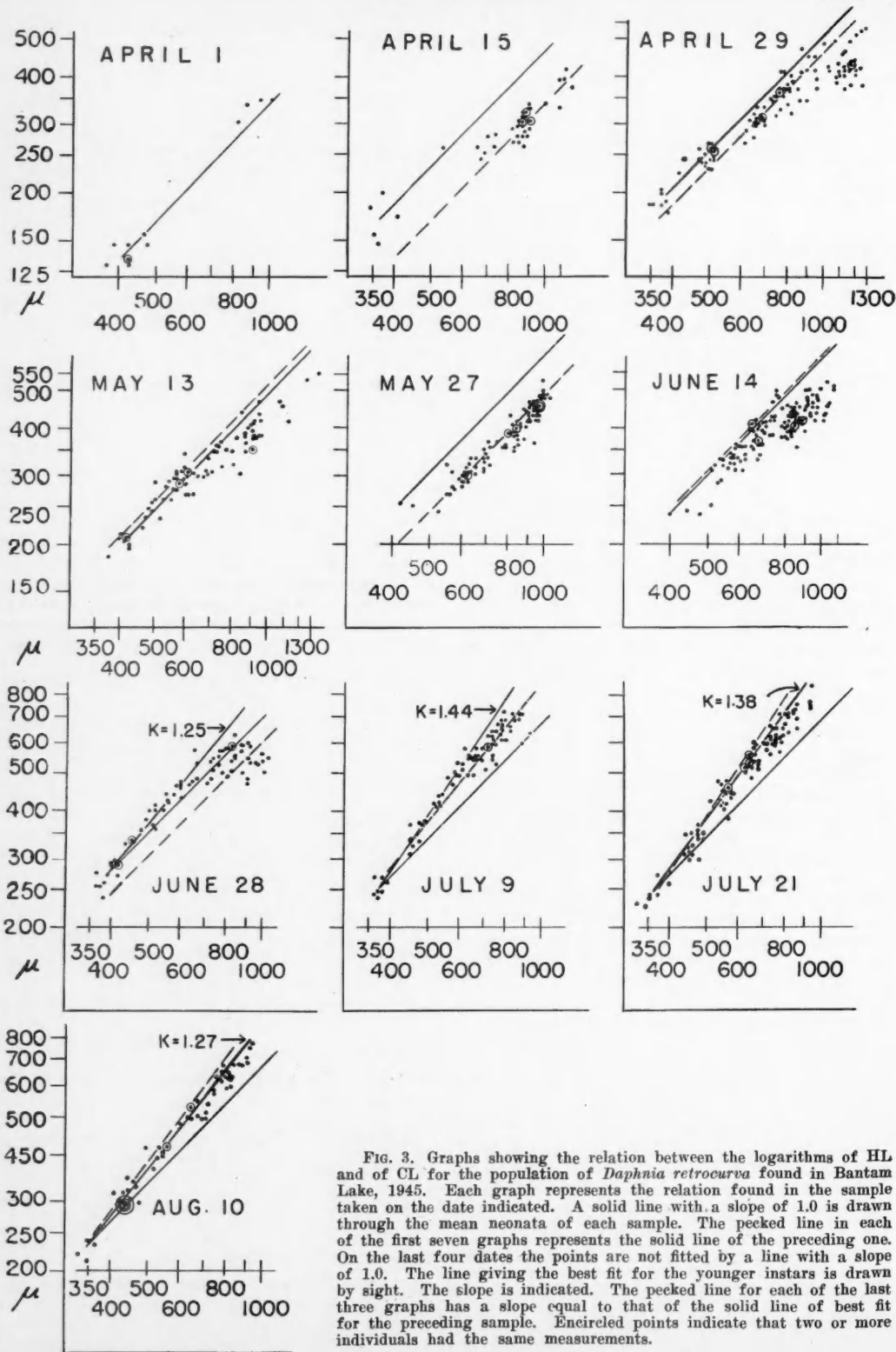


FIG. 3. Graphs showing the relation between the logarithms of HL and of CL for the population of *Daphnia retrocurva* found in Bantam Lake, 1945. Each graph represents the relation found in the sample taken on the date indicated. A solid line with a slope of 1.0 is drawn through the mean neonata of each sample. The dashed line in each of the first seven graphs represents the solid line of the preceding one. On the last four dates the points are not fitted by a line with a slope of 1.0. The line giving the best fit for the younger instars is drawn by sight. The slope is indicated. The dashed line for each of the last three graphs has a slope equal to that of the solid line of best fit for the preceding sample. Encircled points indicate that two or more individuals had the same measurements.

The appearance of the animals comprising the *D. retrocurva* population in Bantam Lake, 1945, is illustrated in Figs. 4 and 5 which are designed to show the growth relations of the various instars. All are camera lucida drawings, at the same magnification, of specimens judged to be average for each instar. Representatives of the instars present in the population on the dates indicated are arranged in horizontal rows. By a careful study of Fig. 3 it is possible to determine, with fair accuracy, the relation between the instars of different samples. The diagonal lines indicate the series of forms through which average neonatae, born at different times, pass.

A cyclomorphic *Daphnia* is one in which the relation of HL to CL varies with time. Therefore in a series of graphs which presents the relation of HL to CL at different times, more than one curve representing this relation must be expected. The older portion of the population will have developed from the young born a week to a month previously, and may resemble the young of previous samples more than the young in the same sample.

Subsequent analysis indicates, as some previous investigators believed, that the progressive form change is in part a function of temperature. Fortunately, for one day, May 27, after the temperature had been nearly constant for a month, the points for HL and CL fall along a single line on the double logarithmic grid, which allows analysis to start from this date. The straight line drawn by sight proves to have a slope of 1.0, meaning that head and carapace are increasing in length at the same relative rate. This suggested that the next step might be to draw a line with a slope of 1.0 on the plot for each date. As there are an infinite number of such lines, the one passing through the point representing the mean HL and CL of the 1st instar specimens (neonatae) was chosen. These are drawn as solid lines in the accompanying figure. As the older individuals might very well be growing like the younger ones of the previous sample, the solid line for each date is carried over, as a pecked line, to the plot for the succeeding date. On the dates for which the points are clearly not on the lines so drawn, defining  $k = 1$ , a second solid line was drawn by sight through the first three or four instars; the slopes of such lines are indicated on the graph.

#### Interpretation

With these lines as guides, we can proceed to analyze the graphs. The April 1 population is composed of very young and old individuals. The old females are presumably ones, born the previous autumn, which have lived over the winter. It is noteworthy that the helmets of these old forms are nearly on the line drawn through the first neonatae of the spring. As subsequent growth of the helmets relative to the carapace of these individuals is isauxetic, prior growth presumably was as well, which indicates that the relative dimensions of the last neonatae of the autumn were very much like those of the first

spring broods. The youngest individuals, which belong to the first instar, have mean  $\frac{HL}{CL} = 0.33$ .

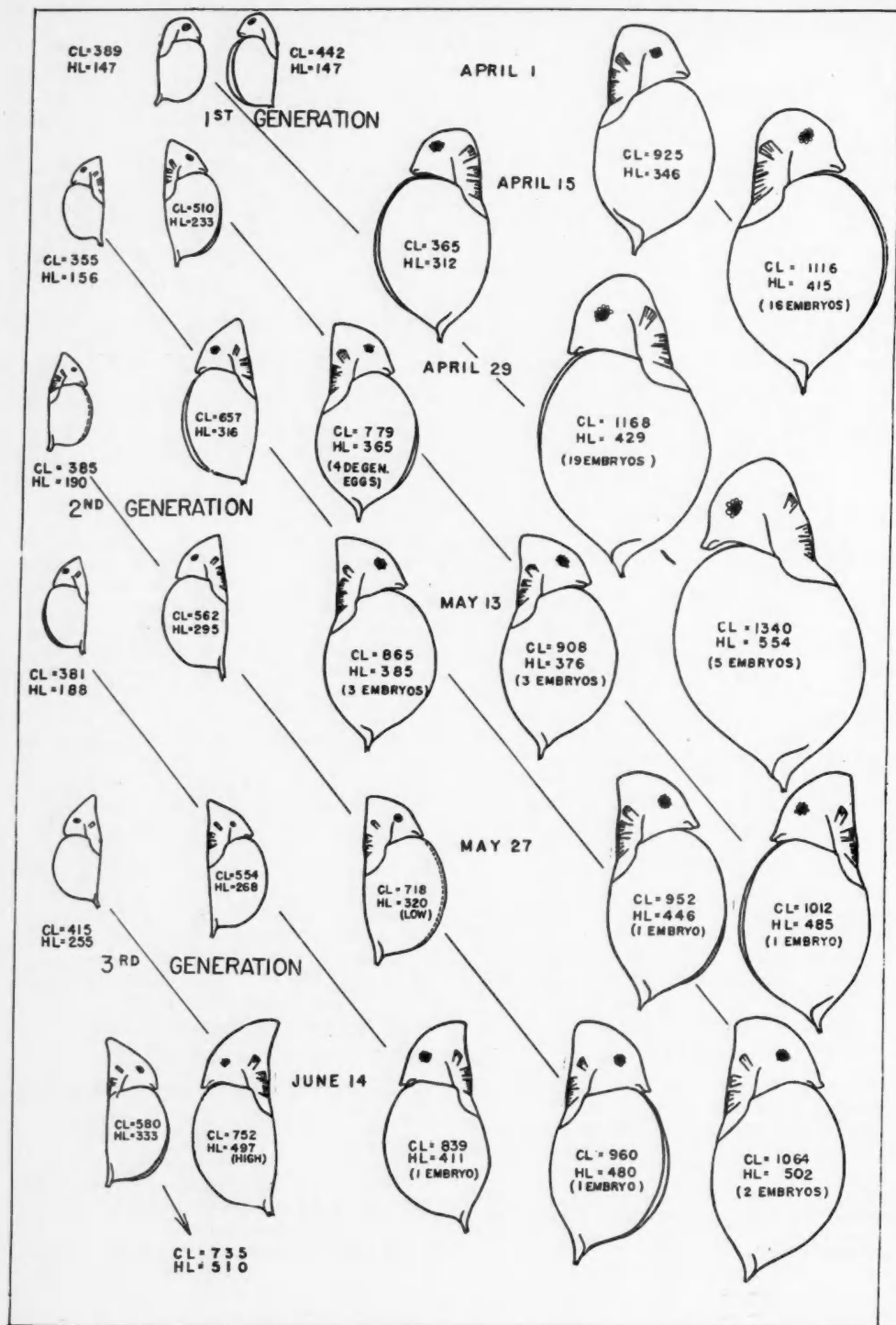
In the sample taken two weeks later more instars are represented. The overwintering females with  $CL = 1100-1200$  (all measurements expressed in micra unless otherwise stated) fall just a little above the pecked line. The points between  $CL = 800$  and 900 represent adult stages of the first offspring of the year, which were in the first and second instars two weeks before. The mean relative HL of the neonatae on April 15 is much higher than that on April 1,  $\frac{HL}{CL} = 0.46$ . While the two groups of smallest individuals appear to have been born with the same  $\frac{HL}{CL}$  ratios, the next oldest forms had  $\frac{HL}{CL}$  ratios intermediate between those characteristic of the April 1 and April 15 neonatae. This is expected if the relative head length increases continuously.

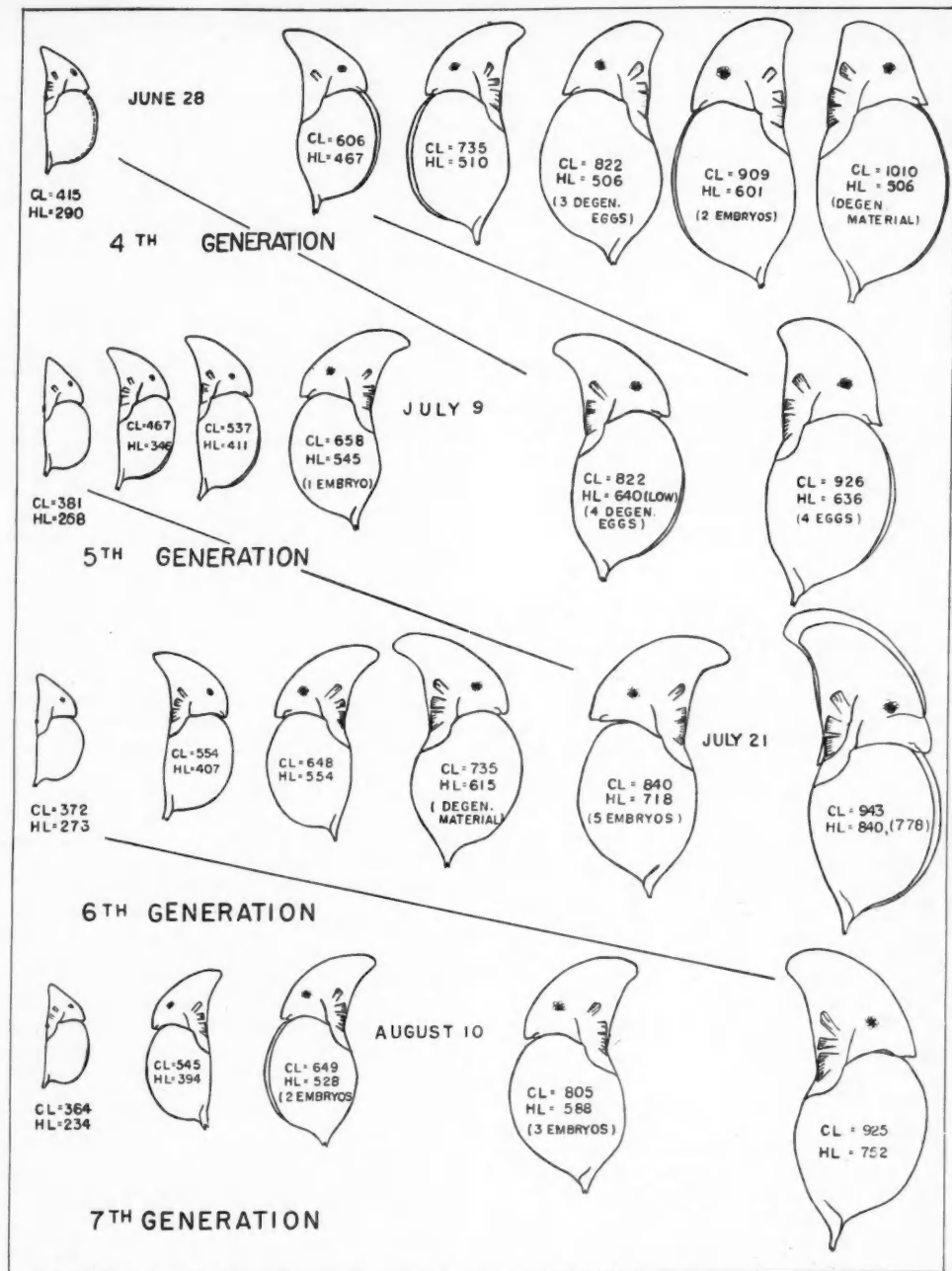
On April 29, there is a group of large adults whose heads are relatively shorter than those of the remainder of the population. These, with  $CL = 1100$  to 1200, are the first adults of the season, whose CL's on April 15 were 800 to 900. Most of the rest of the population above  $CL = 600$  falls along the pecked line. The antecedents of the small group of individuals with  $CL = 1200$  to 1300 and falling just below the pecked line are uncertain. The ratio  $\frac{HL}{CL} = .50$  in the two groups of smallest individuals is greater than that of most of the rest of the population.

On May 13, the young are born with heads relatively shorter than those of April 29. Because of this the relatively tallest heads are carried by those with  $CL$  between 550 and 650, derived from the younger groups of April 29. Above  $CL = 650$  are those whose relative head length is approximated by the pecked line of April 29. The specimen at about 1350 is the largest found in any sample.

On May 27 almost the entire population showed the same relative HL, as indicated by the relation of all but three points to the pecked line. This is due to the fact that all neonatae since the end of April have had nearly the same  $\frac{HL}{CL}$  ratio, and grew isauxetically. There was only one neonata found. For this  $\frac{HL}{CL} = 0.615$  as compared with ca. 0.485 for the remainder of the sample.

Specimens of the population taken on June 14 fall into two groups, with the separation at  $CL = 770$ . Those above this size are the older instars of those of the May 27 sample with  $CL$  greater than ca. 600. The younger group is represented by points falling just below the pecked line of the June 14 graph. This line which was based on the single neonata of the May 27 sample may be too high. As the posi-





FIGS. 4 and 5. Camera lucida drawings of *Daphnia retrocurva* of Bantam Lake, 1945. Drawings of representative sizes for each sample are arranged in horizontal rows. Diagonal lines indicate as closely as possible the developmental stages of each specimen. All are drawn to the same magnification.

tion of the solid line of June 14 is determined by a single neonata, the inversion of the lines is not of the same degree of significance as that of the two lines on the May 13 graph, which are based on larger numbers. Summarizing the discussion to this point, it is clear that up to June 14, the whole of the data can be explained in terms of a variable

$\frac{HL}{CL}$  ratio at birth with isauxetic growth throughout the later instars. With the next sample a new phenomenon is encountered.

The largest adults, later stages of the intermediate instars of June 14, are just below the peeked line of the June 28 plot. The solid line, defining  $k = 1$ , drawn through the mean neonata represents the

$\frac{HL}{CL}$  ratio of a large group of specimens with CL between 750 and 900. Below  $CL = 750$  the relationship is quite different as most of the points fall well above this line and a line drawn by sight through these has a  $k$  value of 1.25. This means that HL, head length, is increasing faster than CL. There has been no indication of tachyauexis in any previous

sample of this season. The  $\frac{HL}{CL}$  ratio for the mean neonata has reached a maximum of 0.704. Moreover, the fact that there is a group of older individuals apparently derived by isauxesis from neonatae of these same dimensions indicates that this tachyauexis followed the attainment of the greatest value

for  $\frac{HL}{CL}$ , a point of considerable interest. Whether this maximum value is the largest possible for this race is not known; it is the highest that was reached during this season.

In the following three samples the head increased more rapidly in length than did the carapace, although  $\frac{HL}{CL}$  ratio of the neonatae decreased slightly.

On July 9 the points below  $CL = 700$  were fitted by a line with  $k = 1.44$ , while those above 700 fell along the peeked line,  $k = 1.25$ . By the time that the population was next studied a line drawn by sight through the points below  $CL = 600$  has a  $k$  of only 1.38, probably a significant drop from the July 9 value. The specimens with CL above 600, which fall below the solid line instead of above as would be expected, are egg-bearing adults. That these adults do not sustain the high degree of tachyauexis manifested by the immature stages is of importance. The amount of decrease which any individual shows does not appear to be connected with the number of eggs or embryos in the brood pouch so that egg production is probably not responsible for the decrease in the relative growth rate. In the last sample of this series, that of August 10, most points fall between the line  $k = 1.38$  and  $k = 1.0$ . A line  $k = 1.27$  was drawn by sight through those below 600. Most of the measurements between  $CL = 600$  and 900 are below this line. This can be attributed to the decrease of the relative growth rate noted above.

Three points of cardinal importance in the understanding of cyclomorphosis emerge from this relative growth analysis.

1. The relative helmet length of the neonatae increases gradually from early spring to a midsummer maximum.

2. These helmets grow isauxetically with respect to the carapace during the first part of the season and later show tachyauexis after the relative neonate helmet length has reached its maximum.

3. The high degree of tachyauexis shown by the younger instars of the July samples is not sustained by the adults.

#### FORM AS A CORRELATE OF TEMPERATURE

Two environmental factors, temperature and nutrition, have been proposed as determinants of cyclomorphosis. Temperature, the more obvious variable, was historically the first to be considered. Wesenberg-Lund's observations (1900, 1908) led him to conclude that temperature was involved in helmet formation. Ostwald's experiments (1904) indicated the importance of temperature in controlling the helmet size of newborn *D. cucullata* in the laboratory. Coker & Addlestone (1938) in more complete experiments proved this true for *Daphnia galeata*. It seemed desirable to study the relation of temperature to helmet formation in both the lake and in the laboratory using animals of the same population. The following discussion is devoted to a consideration of temperature and helmet development in the lake.

Of the two above-mentioned variables, temperature is the more easily measured. At the time of each sampling records of the surface and bottom temperatures were made. The mean of these two is recorded in Table 4 and Fig. 6. In order to gain some insight into the changes in water temperature in the intervals between these records, a solid line is added indicating the fluctuations in air temperature. Daily maximum and minimum temperatures from Waterbury and Hartford, Conn., the two nearest weather stations, differ by only a few degrees Fahrenheit. As Waterbury is nearer to Bantam Lake (14 miles or 23 km. to the S. E. of

TABLE 4. *Daphnia retrocurva*. Neonatae measurements and temperature.

Date	No. present	Mean CL in Micra	Mean HL in Micra	Mean HL Mean CL	k	Mean Water temp. °C.	Water temp. surf. °C.	Water Temp. bot. (6-7m.) °C.
April 1	6	409	136.5	0.334	1.0	8.2	8.20	8.18
" 15	4	360	171	.464	1.0	14.1	14.12	14.10
" 29	9	382	196	.513	1.0	11.6	12.0	11.15
May 13	7	415	202	.487	1.0	11.4	11.57	11.20
" 27	1	415	255	.615	1.0	15.7	16.78	14.60
June 14	1	398	238	.598	1.0	19.6	22.80	16.40
						(19.1)		3m = 18.20
" 28	13	394	277	.704	1.25	19.3	22.10	16.44
July 9	7	375	253	.675	1.44	21.2	24.20	18.10
" 21	8	362	246	.680	1.38	22.5	24.72	20.28
						(22.8)		3m = 23.42
Aug. 10	5	346	228	.659	1.27	?	ca. 20-22?	?



the lake) and at about the same elevation, the air temperatures from this station were used. However, during July these were not available, and those for Hartford were substituted. These maximum and minimum records as published by the United States Weather Bureau were converted into Centigrade readings and the daily mean calculated. These daily means were smoothed by threes and plotted. The lake itself smooths the temperatures even more. An estimation of the fluctuations of the mean water temperature is given as the pecked curve.

#### Relative Head Length of Neonatae

It will be noted (Fig. 6) that both the temperature and the neonate  $\frac{HL}{CL}$  ratio show similar trends. Both rise from April 1 to June and thereafter change less. The magnitude of the differences between the  $\frac{HL}{CL}$  ratios on successive dates is paralleled by that between mean temperatures. Some irregularities, however, are to be noted. Between April 29 and May 13 when there is a well established regression of  $\frac{HL}{CL}$  ratios, the temperature appears to have remained more or less unchanged. It must be noted, however, that the decrease in the ratio is due to a large increase in mean CL, accompanying a small one of HL.

Some discrepancies apparent in Fig. 6 between the two variables are resolved when it is remembered that the relative helmet size of the neonatae found in a sample is not that characteristic of the temperature at the time of sampling. Both Ostwald (*D. cucullata*) and Coker and Addlestone (in *D. galeata*) showed that it is the temperature prevailing during the early and middle periods of embryonic development which determines helmet size. Since the duration of embryonic development is about two days at 21°-24° C., about ten days at 6°-7° C., the mean neonate  $\frac{HL}{CL}$  ratio for any date was determined by the temperature of the lake one to five or six days previous. The mean lake temperature at the critical period can be estimated from the pecked line. When these points are entered on the correlation table (Fig. 7) it is evident that there is a close correlation between these two variables.

The values for the mean carapace length of the neonatae tend to show an inverse relation to the mean water temperature, as can be seen in Fig. 6. The most reasonable interpretation of these changes in size of the neonatae is that they reflect changes in the average size of the eggs. The size of the eggs as observed in the brood pouches does appear to vary, with the smallest ones being found at the higher temperatures. Before egg measurements can be used to test this suggestion the normal stages of development must be elucidated. This inverse relation of neonate size and temperature emphasizes the importance of relative rather than absolute helmet growth.

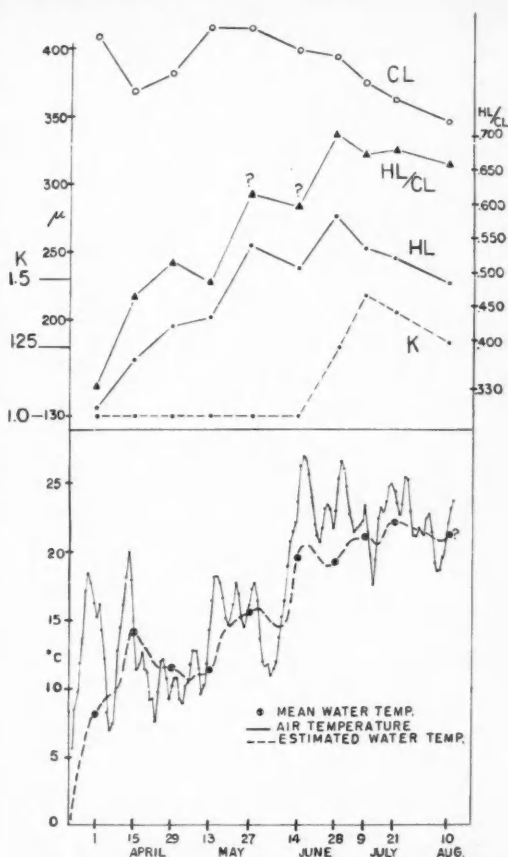


FIG. 6. *Daphnia retrocurva*, Bantam Lake, 1945. Graph showing relationship between temperature, the neonate attributes HL, CL and HL/CL, and the exponent of post-natal relative helmet growth, K. The two questioned values for HL/CL are those based upon single neonatae. See text for explanation of temperature curves.

#### Temperature and Tachyauaxisis

The relation of tachyauaxisis to water temperature is quite different. (Table 4, Fig. 6.) Tachyauaxisis only occurs when the mean temperature is above 19° C. However, on June 14, the temperature was above 19° C. and isauaxisis prevailed. It is possible that the type of relative growth, either isauaxisis, or heterauaxisis, is determined during embryonic development. The water temperature evidently rose rapidly prior to June 14, so that, even if determination was not until two days before birth, the mean temperature would be below 19° C. (probably nearer to 18° C.) during the period in question. Subsequently when the water temperature was continually above 19° C. tachyauaxisis occurred. It is therefore possible that for this race there is a critical temperature ca. 18°-19° C. below which tachyauaxisis cannot occur. For reasons given below this suggestion cannot at present be subjected to experimental verification. Al-

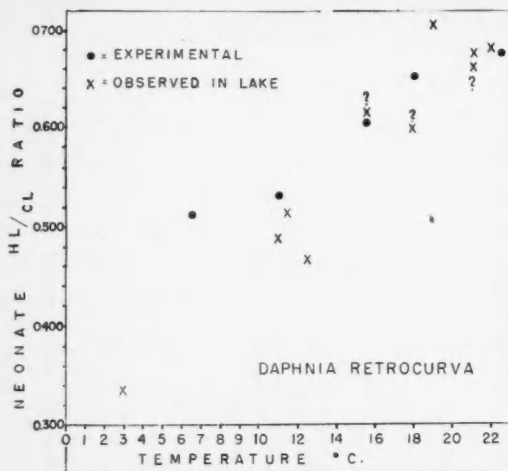


FIG. 7. *Daphnia retrocurva*, Bantam Lake, 1945. Table of correlation between neonate HL/CL ratio and the temperature during embryonic development. The temperatures for the lake are taken from the curve of estimated mean water temperature given in Fig. 6.

though the possibility of a critical temperature is reasonable, there is as yet no certain evidence that tachyauæsis in the lake is directly dependent upon thermal factors.

#### THE INDEPENDENCE OF FORM CHANGE AND THE NUTRITION OF THE POPULATION

The assertion by Woltereck that nutrition is the primary factor controlling helmet size, has been disputed by Wesenberg-Lund. It is therefore necessary to investigate this relation.

Obtaining an accurate estimate of the state of nutrition of a natural population is a difficult task. There are two general methods of attacking such a problem. Quantitative and qualitative examination of the gut contents can be made. If the type of food on different days is similar, than the quantity present in the gut will give a rough indication of the amount assimilated. Qualitative differences complicate the interpretation. The other approach, from quite the opposite direction, is to study changes in the organism which are likely to be dependent upon the amount of food assimilated.

In the transparent bodies of *Daphnia*, the contents of the gut are easily seen. Their appearance during life and after death was noted, and microscopic examination of this material gave a clue to the identity of the nannoplanktonic elements comprising the food. In addition there are three measurable variables, namely the pre-adult size increment, the mean number of eggs produced and the percentage of adults with degenerating eggs, which may be reasonably supposed to reflect the nutritive condition of the population. More will be said about each of these criteria in subsequent paragraphs.

#### Gut Contents

An attempt at an objective quantitative comparison of gut contents at different times was made in the following manner. Fifteen to twenty medium sized adults chosen at random were mounted on a slide. The outline of the gut, in the ten in which the guts were least obscured, was drawn. Three types of shading were used to depict the contents of the gut and indicate its relative abundance. As can be seen in Fig. 8 the guts were most nearly full on April 1 (only 3 individuals found) and May 13. They were less full on April 15, 29, May 27 and June 28; still less on July 21 and Aug. 10, and practically empty on June 14 and July 9.

An attempt was made by careful microscopic examination to determine the phytoplanktonic elements comprising the gut contents. Several medium sized adults were selected from the samples of April 29, June 14 and July 21. The major portion of these contents could not be recognized. Of the remainder there was a fair amount of an *Aphaenocapsa*-like form ca. 1 micron in diameter, and a spherical green alga occurring either as single individuals (5-10 micra in diameter) or clumps of as many as 6 together on April 29. On this date colonial spherical green algae were abundant in the phytoplankton and the *Aphaenocapsa*-like form was common. Although there were small numbers of diatoms of the genera *Fragilaria*, *Tabellaria* and *Asterionella* present in the lake water, no diatom tests were found among the gut contents. Solitary spherical green algae, which were numerically superior in the lake on June 14, and the fairly abundant *Aphaenocapsa*-like form were the only organisms which could be identified in the nearly empty guts of this date. Similarly on July 21, the same two types of phytoplankters were the only recognizable components of the food of *Daphnia retrocurva*. The solitary spherical green alga, dominant on June 14, was rare in the lake. Some colonial green algae were still present. The blue-greens (several species of *Anabaena*, several of *Microcystis*) and desmids (esp. *Xanthidium*) were dominant. There was a large amount of organic detritus suspended in the water possibly derived from the decomposition of the large blue-green algae. This detritus may have been utilized by *Daphnia* as food, although it cannot be identified in the gut. If it was eaten, it is the only departure from the qualitatively monotonous food hitherto utilized. Kastal'skaia-Karzinkina (1942) (seen in abstract only) found that flagellates, small green algae and some bacteria are easily digested by *Daphnia*—species not named in abstract. *Scenedesmus*, *Raphidium* and *Pediastrum* were poorly digested.

#### Pre-Adult Growth

Banta, Ingle, & Wood reported (Banta, 1939) that individuals of *Daphnia longispina* reared with limited food were smaller at the fifth instar (1st adult) than were others of the same clone kept at the same temperature but given unlimited food. How-

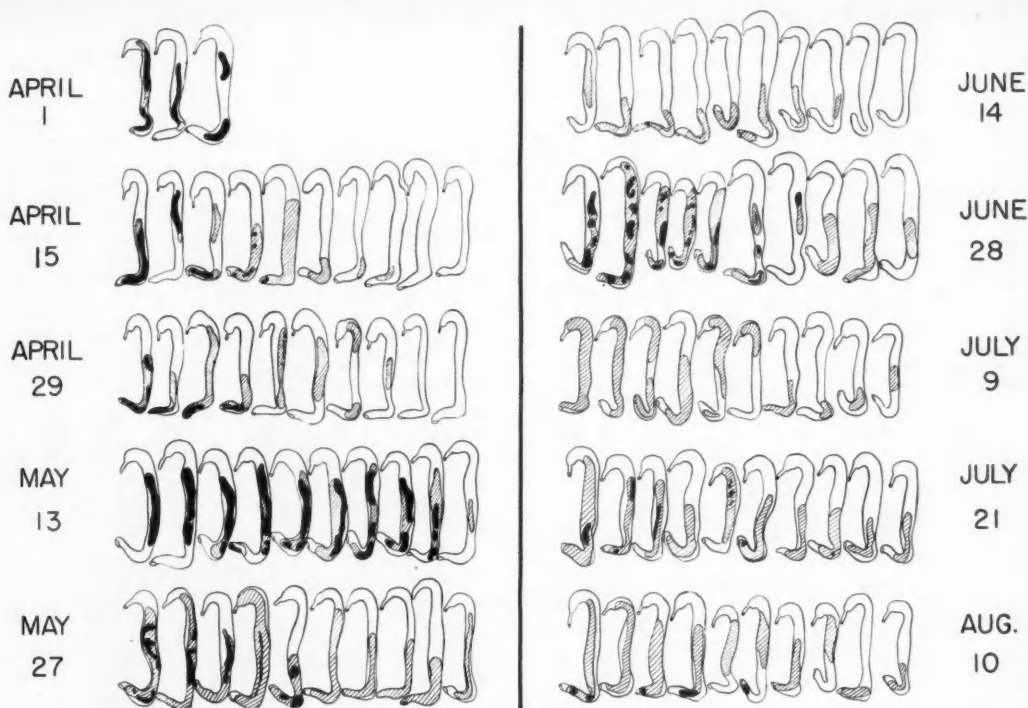


FIG. 8. Quantitative comparison of gut contents, *Daphnia retrocurva*, Bantam Lake, 1945. The guts of ten adults picked at random were drawn for all except the April 1 sample. Only three specimens were available here. Portions of the gut apparently empty are indicated by the unshaded areas. Dense food masses are indicated in black. The hatched areas are occupied by intermediate concentrations of food.

ever, comparison of the sizes of the first ovigerous females of *D. retrocurva* at different times of the year will not be a measure merely of nutrition. Both the size at birth and the effect of temperature must be taken into consideration. Instead of using the length of the first adult instar, the increase in length of the carapace from the neonatae to the smallest ovigerous females has been used without reference to the question of instars and the numerical designation of the first ovigerous one. This increment is found by subtracting from the mean CL of the five smallest egg-bearing individuals their mean CL at birth as determined from Figure 3. The values are given in Table 5 and Figure 10.

The values for samples prior to June 14 are much higher than those for subsequent ones. These lower values obtained at temperatures between 19°-22° C., the former between 11°-14° C. Laboratory cultures with unlimited food at different temperatures furnish a means of compensating for the effect of temperature on the CL increase during the pre-adult instars (probably through its effect on rate of ovarian development). There is one record (Exp. 2, Table 13) at 6°-7° C. in which the CL is 390 micra, and one for 11°-12° C. (Exp. 4, Table 13) where it is 425 micra. For temperatures of 21°-24° C., which are more interesting there are about

a dozen pertinent records (Exps. 6-13, Table 13) in which the CL increase ranges from 320 to 363 micra with a mean of 346. These will serve as an indication of the increase which is made with ample nutrition.

The laboratory cultures at 11°-12° C. showed the same increment as was found in the lake on April 15, May 13 and 27, under similar conditions. This is taken to indicate that nutrition was good at, or had been good just prior to, these dates. The decrease in the pre-adult growth increment between May 27 and June 28 may be due largely to the in-

TABLE 5. *Daphnia retrocurva*. Calculation of pre-adult growth increment. All values in micra.

Date	Mean CL of 5 smallest adults	Mean CL when neonatae	Mean increase in CL from neonatae to adults
April 15.....	825	409	416
" 29.....	746	369	377
May 13.....	812	382	430
" 27.....	851	415	436
June 14.....	793	410	383
" 28.....	737	392	345
July 9.....	644	385	259
" 21.....	633	370	263
August 10.....	652	355	295

crease in temperature. However, the low values on July 9 and 21 indicate that nutrition was inadequate, as the growth in the lake was well below that achieved in laboratory cultures at about the same temperature. Between July 21 and August 10, the population appears somewhat better fed, as the growth increment approaches the level of the lowest values found in laboratory cultures.

#### Egg Production

After the attainment of maturity the growth of the body from instar to instar is much less than it was previously and a large part of the food assimilated is utilized in egg formation. Hence the number of eggs should be a criterion of nutrition. To compare nutrition at different times by this method, the number of eggs and embryos found in the brood pouches of the adults are summed and divided by the number of adults present. This gives the mean number of eggs produced per adult for a short interval just preceding the sampling (Table 6). A plot of these values shows a sharp maximum at April 29 with the mean number of eggs produced at subsequent times trifling in comparison. However, on April 29 there occurred in the population numerous individuals larger than any occurring at other times and with very large broods. It seemed that a more accurate measure of nutrition might be the egg production by adults of approximately the same size.

TABLE 6. *Daphnia retrocurva*. Egg production. Calculation of mean number of eggs produced per adult.

Date	Total Number Adults Meas.	Total Number Eggs	Eggs per Adult	Adults 778 < CL < 952 Micra	Number Eggs for these	Eggs per Adult
April 1	4	0	0.0	3	0.0	0.0
" 15	37	214	5.79	27	153	5.67
" 29	54	559	10.36	22	135	6.14
May 13	29	91	3.14	21	63	3.00
" 27	47	43	0.91	34	24	0.71
June 14	56	42	0.75	43	27	0.63
" 28	24	45	1.87	15	28	1.86
July 9	41	58	1.41	17	29	1.70
" 21	47	121	2.57	19	56	2.95
Aug. 10	26	54	2.08	12	27	2.25

For this reason the adults were divided into groups on the basis of the CL measurements, and the mean number of eggs or embryos carried by individuals within these groups calculated. The results of this analysis are shown in the histogram, Fig. 9. The mean number of eggs produced by adults with carapaces between 778 and 952 micra in length, the greatest range of sizes present in all samples, was calculated for each sample. These values are given in Table 6, plotted in Figure 10. Except for April 29, it follows closely the curve for egg production by all adults. The lowest rates of egg production were found on May 27 and June 14. After June 14, egg production increased gradually, but reached at best only about one-half the magnitude of the peak of April 15 and 29.

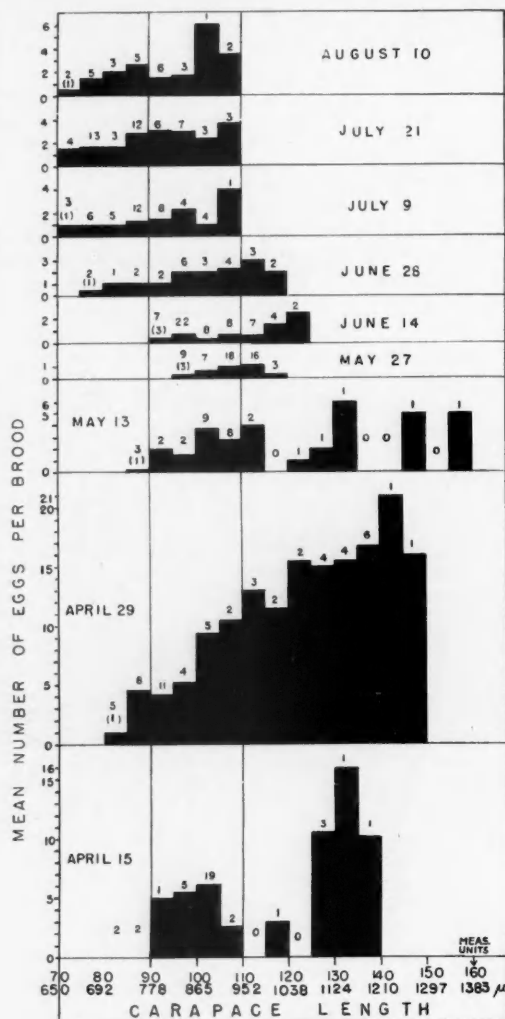


FIG. 9. *Daphnia retrocurva*, Bantam Lake, 1945. Histograms indicating mean egg production for adults of various sizes. The size range between CL = 778 and 952 micra is marked off to facilitate comparison of different samples. The small numerals above each bar give the number of adults upon which each mean value is based.

If the number of eggs produced were governed by the level of nutrition, the curve would indicate that the *Daphnia* were best fed during April, poorest during the last week of May and the first half of June, with nutrition slowly improving thereafter. There appears to be a complicating factor, however, which is made evident by the large numbers of eggs in the broods of the large adults of April 15 and 29. The presence in the spring and at no other time of such large females with large numbers of eggs has been noted numerous times in populations of many species of *Daphnia* (and other Daphnids as well). An ex-



planation given by Wesenberg-Lund when noting this phenomenon in the *Daphnia* populations of Danish lakes seems reasonable.

In my opinion this variation in the number of eggs in the egg-sets is not to be interpreted, that the spring individuals in contrast to the individuals of all other seasons are remarkable for a specially high fertility. I am much more inclined to believe that the spring forms yield the whole number of eggs in one or very few egg-sets, each consisting of a very large number of eggs, but the summer forms in a very great number of egg-sets, each of one or a few eggs. (1908, General Part, p. 245.)

Temperature during the egg-laying period probably controls this in a manner as yet incompletely understood. This same explanation probably accounts for a large part of the high egg/brood values for adults with CL between 778 and 952 micra at that time. The relative effect of nutrition on egg production during April is hence undetermined.

Leaving aside this unexplained phenomenon, there is some evidence that the poor nutrition did restrict the egg production later in the season. Four adults collected on June 14 (CL = 88, 95, 102 micrometer units when taken) were reared in the laboratory in filtered lake water to which an adequate amount of the algae-bacteria culture had been added for food. Whereas the guts of these specimens in the lake on June 14 had been practically empty, they soon acquired a light green color due to the algae in gut. Within the next 12 days, at a temperature of between 21°-24° C. these individuals produced 39 eggs. A comparison of mean egg production/instar in different size ranges with that in the lake on June 14 can be made. As carapace measurements for some instars were omitted, the degree of subjectivity necessary in grouping the sizes by fours is obviated by using more inclusive groups of 9 micrometer units. The mean egg production/adult in the lake on June 14 is easily cast into this new system. The comparison is given as Table 7. The numbers in parentheses give the number of specimens on which each average is based.

TABLE 7. *Daphnia retrocurva*. Comparison of mean egg production/individual in lake (June 14) and in laboratory cultures (June 15-27). Numbers in parentheses are those upon which each mean is based. 1 micrometer unit = 8.65 micra.

CL group (micrometer units).....	Mean Number Eggs / Adult			
	90 - 99	100 - 109	110 - 119	120 - 129
Lake—June 14.....	0.72(25)	0.5(18)	0.91(11)	2.5(2)
Lab.—June 15-27.....	2.0(2)	3.0(3)	5.66(3)	4.5(2)

Although the number of specimens in laboratory culture was small, the mean number of eggs they produced is strikingly greater than that produced in the lake. The mean egg production in the lake for all sizes was 0.75 eggs/individual, based on 56

adults. The guts of the *Daphnia* in the lake were emptiest at the time of this minimum of egg production. In laboratory culture 39 eggs were produced in a total of 10 instars, an average of 3.9 eggs/instar. As the egg production of a *Daphnia* from the lake is known only for the instar caught, egg production/individual in the lake can be considered egg production/instar.

Six adults (Flasks Nos. 5, 6, 7, 8, 9 and 11) taken from the tow of June 28 were cultured under conditions similar to those just described for June 14. After the first molt in the laboratory, their carapace lengths ranged from 85 to 100 micrometer units. From June 29 to July 7 these six specimens passed through a total of 15 adult instars, producing a total of 49 eggs. This is a mean egg production of 3.27 eggs/instar, as compared with that of 1.87/individual for the 24 adults measured from the June 28 sample. A breakdown of mean egg production/individual into size groups is seen in Table 8.

TABLE 8. *Daphnia retrocurva*. Comparison of mean egg production/individual in lake (June 28) and in laboratory cultures (June 29-July 7). Numbers in parentheses are those upon which each mean is based. 1 micrometer unit = 8.65 micra.

CL group (micrometer units)	Mean Number Eggs / Adult						
	85-89	90-94	95-99	100-104	105-109	110-114	115-119
Lake—June 28	1.0(2)	0.5(2)	2.0(6)	2.0(3)	2.25(4)	3.0(3)	2.0(2)
Lab.—June 29-July 7	1.0(1)	.....	2.5(2)	2.66(6)	5.0(4)	2.0(1)	5.0(1)

The mean egg production in the laboratory of 3.27 eggs/instar for specimens taken on June 28 compares with the value of 3.9 eggs/instar for those collected two weeks previously and with that in the lake on May 13 (3.14 eggs/adult). It will be recalled that on this last date (May 13) nutritive conditions in the lake were optimal. If we restrict the comparison to the CL range of 90-109 micrometer units (778-952 micra) we find that mean egg production/instar in the laboratory cultures was 2.6 and 3.4 eggs/instar for June 14 and June 28 resp. and 3.0 for the adults in the lake on May 13.

This evidence, although not conclusive, strongly indicates that, excluding the first generation, three eggs are produced on the average at each instar in the range specified above, when nutritive conditions are favorable. The depression below this level on June 14 and 28 appears to be due primarily to lack of food, and there is no reason to believe that the low values on May 27 and July 9 are due to any other factor.

#### Egg Degeneration

During examination of living material from the June hauls it was noted that the eggs and embryos had less of the green-gray color characteristic of well fed animals in the laboratory, some being nearly colorless. Among these colorless eggs it was further



noted that some had lost their hyaline appearance and were, indeed, degenerating. The first sign of this breakdown was a gathering of clear drops near the large central oil drop, with diffraction of light at the surface of these drops producing a dark gray color. Rupture of the egg membrane, with the several pieces rolling up into tight coils, accompanied the early stages of degeneration. After this followed the breakdown of the whole egg into an irregular gray mass, which soon disintegrated completely. It is of interest that some of the eggs of the other races of *Daphnia* present were also noted to be degenerating at the times of the maximum amount of degeneration of *Daphnia retrocurva*. Percentages for these smaller populations were not determined. No reference to such degeneration of eggs in a natural population has been found. Ostwald (1904) in his attempts to culture cyclomorphic *Daphnia cucullata* found that when food was inadequate most of the eggs laid by his experimental females failed to develop. This phenomenon to which he applies the word "abortieren" appears to be identical with that here designed by "degeneration." Furthermore, his feeding the *Daphnia* triturated diatoms as food increased egg production but did not appear to cause any decrease in the amount of degeneration. Banta (1939) mentions in a footnote (page 46) that degeneration of eggs in *Simnocephalus*, *Moina* and *Daphnia* may occur under "very unfavorable" culture conditions (overcrowding?, inadequate food?).

The only degenerating eggs seen in laboratory cultures were those produced by females shortly after being taken from the lake at the time of the June maximum of degeneration. On June 15, five cultures were started, each with one adult female taken the previous day. Each had one egg or embryo in her brood pouch. Most of the females in the lake carried a single egg or embryo at that time. An ample amount of the algae-bacteria mixture was added to each culture. One animal died in a few days. The other four produced at the next molt 4-6 eggs apiece, some or all of which died before birth. After each of the following two or three molts the females produced about the same number of eggs, but the amount of degeneration decreased. Within two weeks all eggs were viable. Concomitant with the increase in viability, the guts of the mothers changed from the pale yellow of near emptiness to a bright green color due to the ingested green algae. The color of the eggs showed a similar transition from the paleness which characterized many of the eggs in the lake to the deeper coloration typical of the eggs of well fed mothers. In this latter state, the egg is a deep gray-green with a deep yellow or orange oil drop in the center. The yellow-orange color of the oil drop is undoubtedly due to carotinoid pigments. The gray-green is possibly a chlorophyll derivative (McTeal 1945). This coloration is found in both lake and laboratory with adequate nutrition.

Casual observations throughout the investigation indicate a high correlation between pale color of eggs and subsequent degeneration. A number of

adults taken alive on June 28 were examined to ascertain the incidence of egg degeneration, as mentioned below. Any extremes in coloration were noted. Of the 92 females examined, 16 had eggs in early stages of development. The oil drops of 6 of these were described as "orange" or "very orange." Three were "pale." The coloration of others is not recorded. Thus one fifth of the eggs were pale. There were 45 broods of embryos, of which none were recorded as being exceptionally pale, while 21 had deeply colored oil drops. Twenty-six broods consisted entirely or in part of degenerating eggs, which amounts to 36% of the later stages. It would appear that all of the "pale" eggs, and some others as well, had proved inviable.

It was felt that the incidence of this degeneration might afford a criterion of the state of nutrition. The number of adults whose brood pouches contained degenerating eggs, expressed as a percentage of the total number of adults, was taken as the most suitable measure. Some broods contained both degenerating and normal eggs; these were counted as showing degeneration. The total number of degenerating eggs, as opposed to normal ones, cannot be used because all semblance of form is lost in late stages of disintegration. All of these values are based upon examination of preserved material. To ascertain whether inspection of living material would reveal the same percentage of degeneration, a vertical tow was made on June 28, at 12:30 p.m. This was taken to the laboratory and examined from 2:45-9:30 p.m. the same day. Of the 92 adults examined, 26 had broods showing signs of degeneration. The 28.3% thus obtained agrees closely with the 29.1% of degeneration found in the 24 preserved specimens of that date. The percentages given in Table 9 are plotted in Figure 10.

TABLE 9. *Daphnia retrocurva*. Degeneration of eggs.

Date	Number Adults Examined	Number Adults with Broods showing Degen.	Percent with Degen. Broods
April 1.....	0	0	0.0
" 15.....	36	3	8.33
" 29.....	134	60	44.8
May 13.....	29	2	6.9
" 27.....	53	16	30.2
June 14.....	60	34	56.8
" 28.....	24	7	29.1
July 9.....	40	14	28.6
" 21.....	59	11	18.6
August 10.....	26	3	11.5

#### Estimated Variations of Nutritive Level in Lake

We may now attempt to integrate the knowledge gained by showing the fluctuations of these criteria of nutrition (Fig. 10) and find how nutrition itself varied. When nutrition is good we will expect the guts to be fairly full, the pre-adult growth increment to at least approximate that shown in laboratory culture at the same temperature, egg production to be relatively high and the percentage of broods showing degenerating eggs low.

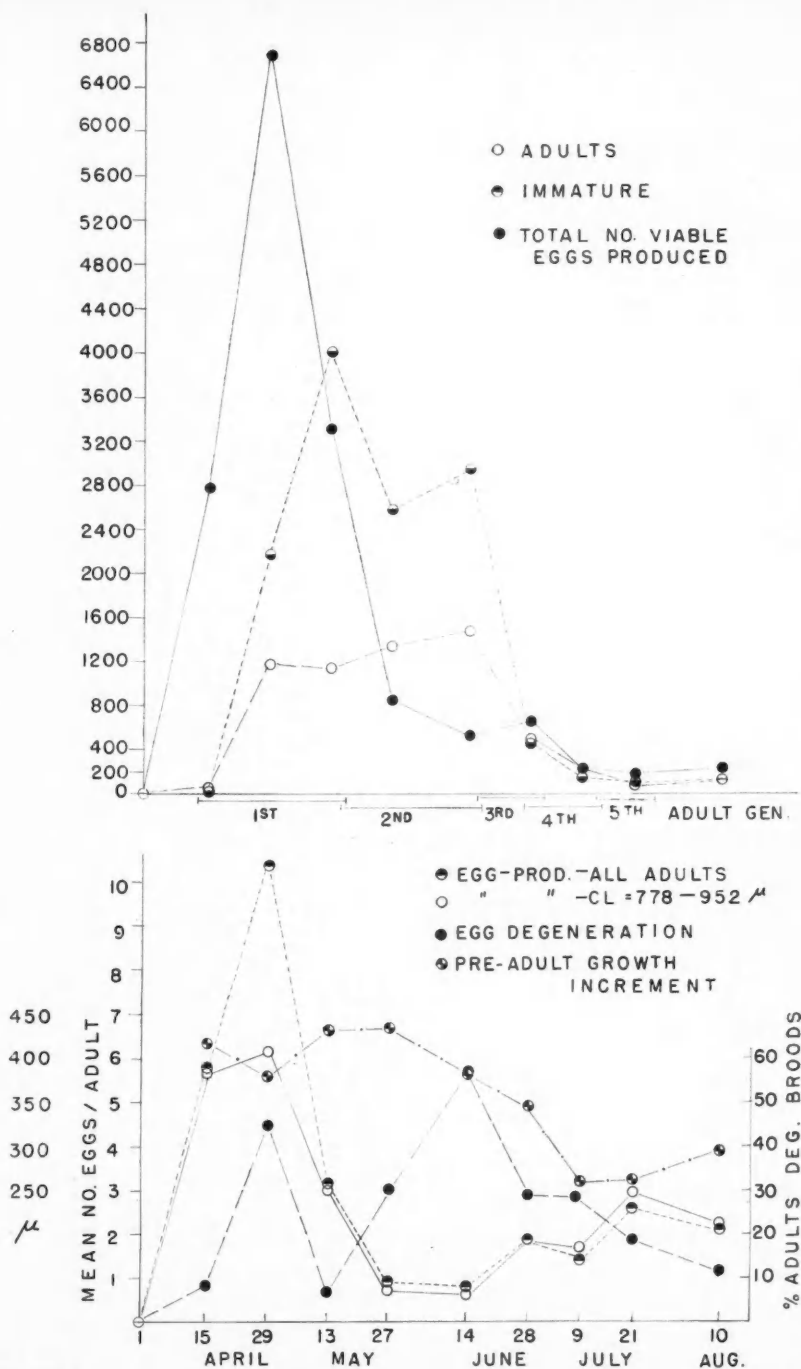


FIG. 10. *Daphnia retrocurva*, Bantam Lake, 1945. Graph showing in lower panel concomitant changes in egg production, egg degeneration and pre-adult growth increments. In the upper portion several aspects of the population dynamics are presented for comparison with the above-mentioned variables. These values are on the basis of equivalent vertical series of plankton trap samples. (See text.)

On April 15 and May 13 the necessary conditions for adequate nutrition appear to have been fulfilled. It is to be remembered that egg production values for first generation adults are primarily determined by factors other than nutrition. In the April 29 sample, the guts contained about as much as they had two weeks earlier. The small decrease in pre-adult growth may signify a slight decline in nutrition. It is strange to find that egg degeneration had increased eight-fold over the previous sample. One of the maxima of egg degeneration thus coincided with the maximum of egg production. That this was mere coincidence seems unlikely, but its significance is at present unknown. The suggestion might be made that egg production was so great that there was not a sufficient amount of some substance necessary for normal development being absorbed by the gut to provide each egg with the minimal amount. This very hypothetical suggestion is at least in accord with the conditions indicated by a comparison of egg production on April 29 and May 13. On the second date both the more abundant gut contents and the greater pre-adult growth increment point to increased nutrition. Temperature had changed but little. The egg production had fallen to one half of the April 29 level, due presumably to factors other than nutrition, and egg degeneration had dropped from 44.8 to 6.9%.

On May 13 nutrition seemed to be as good as it was at any time in the season, but one month later it appeared to be the poorest. The May 27 sample was intermediate between these extremes. At this time the pre-adult growth increment was still as great as it was on May 13, while egg production had dropped to a minimum on May 27 and June 14. It is noteworthy that the only males ever seen in this population were three young ones found on May 27. Male production in *Daphnia* is associated with overcrowding and poor nutrition. (*Vide* Banta, 1939, for summary.) The amount of egg degeneration at the end of May was intermediate between the minimum of May 13 and the maximum of June 14. This second peak in the egg degeneration curve coincided with the minimum of egg production. As the guts appeared quite empty it would seem that in this instance the low nutritive level was responsible both for low egg production and the great amount of egg degeneration.

This state of extreme depression had been alleviated by June 28. The guts contained more food than they had a fortnight before and egg degeneration had halved. Egg production had trebled. Due to the effects of temperature on pre-adult growth a comparison of the increment for the pre-June 14 period with that of pre-June 28 one is of undetermined significance. However, during the interval between June 28 and July 9 this improvement in nutrition underwent a slight reversal. Guts on July 9 were nearly as empty as they had been on June 14. The pre-adult growth increment decreased sharply from June 28 to July 9, while the average temperatures for the corresponding growth periods had in-

creased only by one degree C. The drop in egg degeneration was checked.

After July 9 nutritive conditions showed a slight improvement. The guts contained more material, egg degeneration gradually decreased, and the pre-adult growth increment reached a higher value by Aug. 10, but was still well below the June 28 level. Egg production rose on July 21 to the May 13 level (also achieved in the laboratory) but dropped on Aug. 10.

A few final words should be said concerning the validity of the four criteria of nutritive level. Egg production by adults of the first generation of the season cannot be compared with that of other generations in a comparative study of nutrition. The presence of a maximum of egg degeneration associated with this maximum of egg production is not of the same significance, as a measure of nutrition, as that which occurred later. During periods of rapid temperature change the changes in the pre-adult growth increment are of little value. With these exceptions there is a satisfactory correspondence of the information provided by each of these methods for the evaluation of nutritive changes.

With this picture of nutrition in mind, it remains to compare it with the two processes involved in helmet production. The curve for the mean  $\frac{HL}{CL}$  ratio

of neonatae shows no fluctuations which can be correlated with concomitant ones in nutrition. The only reversal of the general upward trend occurred between April 29 and May 13, within a period of falling temperature, during which nutritive conditions showed every sign of being maximal. The maximum neonate  $\frac{HL}{CL}$  value was maintained from

June 28 to Aug. 10 at a level of nutrition which fluctuated from inadequate to more nearly adequate. Tachyauysis began between June 14 and 28 under conditions of slightly rising nutrition and strongly rising temperature. Between June 28 and July 9 when *k* rose to a maximum of 1.44, the level of nutrition appeared poorest of any time during the period of tachyauysis. The subsequent decline in *k* between July 21 and August 10 occurred while the nutritive level was being maintained. There is no evidence for any relationship between nutrition and either relative neonate head length or tachyauysis.

#### SUMMARY OF CORRELATIONS WITH TEMPERATURE AND NUTRITION

In a general summary of the correlations with temperature and nutrition the following points should be emphasized:

1. There is a close correlation between mean lake temperature during embryonic development and both the absolute and relative head length of the neonatae.
2. Tachyauysis occurred only when the mean lake temperature during embryonic development was above 19° C. but there is no evidence that the value of *k* is controlled by temperature.
3. Nutritive conditions in the lake at least after

the middle of May were below the level easily maintained in the laboratory.

4. Fluctuations in the general level of nutrition bore no apparent relation either to changes in neonate head length or to the rate of tachyauetic growth of the head with respect to the carapace.

#### POPULATION DYNAMICS

It will be well at this point to summarize explicitly several aspects of the population implicitly drawn into the discussion of other phenomena. The remarks which follow can all be deduced from the data presented in Figure 3 and Tables 6 and 9. It will be desirable first to gain an idea of the number and duration of the generations in the period covered.

The small adult population of April 1 is composed of females which have lived over the winter. Reference to Fig. 3 shows that two weeks later the first brood of off-springs from these have matured and comprise the major part of the adults. These are the adults of the first generation, with CL's of 800-900 (all CL measurements in the following discussion expressed in micra). Some of the overwintering females are also present. Most of the eggs are produced by the first generation, hence are of the second generation. Most of the first instar individuals of this date probably belong to the first generation, as the eggs of the first generation adults have not had time to hatch. The intermediate instars are from later broods of offspring of the overwintering females and also belong to the first generation. On April 29, individuals with CL = 750 are mature and, except for a few of the largest which may be overwintering females, belong to the first generation. With little doubt the two smallest instars, as well as all unhatched eggs and embryos, can be assigned to the second generation. On May 13 it appears that mature individuals (CL = 800) belong to the first generation, most members of the second having reached the pre-adult instar only, due to the slow growth at 11° C. However, a few of the smallest ovigerous females belong to this second generation. As most of the eggs are being produced by adults with CL = 778-996, the greater part of the neonatae belong to the second generation. The passage of two weeks sees the disappearance of the first generation. The entire reproductive portion of the population (above CL = 850) belongs to the second generation. A part of the relatively small number of neonatae can probably be assigned to the third generation, although the intermediate sizes belong to the previous one. On June 14 there is a clear separation of adults of the second generation from intermediate instars of the third. The second generation, present in such prodigious numbers on this date is completely missing two weeks later. The sudden rise in temperature between June 14 and 28 is presumably the cause of the rapid turn-over in the population. The large number of *Daphnia* of intermediate size (third generation) is represented by the small number of points below the peaked line of June 28. The major

portion of the adults, clustered at the upper end of the solid line, were born after June 14, apparently soon thereafter. They undoubtedly are offspring of both the second generation adults which were present on June 14 and the third generation which matured shortly after. The reproductives of June 28, then, belong to the third and fourth generations, and the neonatae to both fourth and fifth generations. The older individuals showing tachyauexis appear to be predominantly of the fourth generation. Assignment of portions of the population to generations on subsequent dates is uncertain, as development is so rapid. However, since individuals in laboratory culture at 21°-24° C. developed from egg to maturity in eight to eleven days, the following designations can be inferred. The adult portion of the July 9 population embodies individuals of the immature instars of June 28. Their offspring, the neonatae of this date, are largely of the fifth with some of the sixth generation. There is no confirmation of Woltereck's contention that maximum helmet size in *Daphnia cucullata* is attained only with a certain generation. It is quite clear from this analysis of *D. retrocurva* that the factors determining helmet size are independent of generation number. Had high temperatures developed in the early part of June, there is every reason to believe that the maximum helmets would have been borne by the third and fourth generations. Mature individuals of July 21 are primarily of the fifth generation, and the majority present on Aug. 10 belong to the seventh.

The extent of the adult generations is indicated by the lengths of the bars in Figure 10. The generation number of the neonatae will be one greater than that of the adults for the same date. This arrangement will facilitate the following discussion. In Figs. 4 and 5 the diagonal lines are labelled with the generation number. This furnishes an approximate conception of the appearance of the generations which were present at different times of the season. It must be reiterated that there is no evidence of causal relation between generation number and relative rate of helmet growth.

When the variation of the mean number of eggs per adult is examined in conjunction with the duration of the instars, it is immediately apparent that only the adults of the first generation produce the maximal number of eggs. On April 15 the first mature individuals born in the spring produced mean clutches of just under 6 eggs. On April 29, adults of the same size, i.e. CL between 778 and 952, also of the first generation though born later, similarly produced mean broods of just over 6 eggs. The drop to one-half this amount on May 13, when the adults in the specified size range are undoubtedly of the second generation, is a phenomenon of great interest and of obscure cause. We have seen that there is every indication that there was a simultaneous improvement in nutritive conditions and no change in temperature. Reference may again be made to Wesenberg-Lund's explanation (vide supra p. 427).



We now turn to a consideration of the variations in the actual size of the population. Table 10 and the upper panel of Fig. 10 give the total numbers of adult and immature *Daphnia retrocurva* for each date of sampling. It will be recalled that two 10-liter plankton trap hauls about a meter and a half apart horizontally were taken at depth intervals of one meter from surface to bottom. All specimens in each haul were counted and the mean of the two was taken as characteristic of that depth. The sum of these means gives the total number in a mean vertical series of hauls. As the vertical series were made in the same manner each time, the totals of each mean vertical series will represent similar portions of the entire population present in the lake.

TABLE 10. *Daphnia retrocurva*. Population dynamics. All values are given for equivalent vertical series of plankton trap catches. Volume of water sampled in each series is 160 liters.

Date	Immature	Adults	Total Eggs Produced	Total Viable Eggs
April 1.....	2	1	0(?)	0(?)
" 15.....	20	55	3,190	2,770
" 29.....	2,163	1,170	12,130	6,695
May 13.....	3,999	1,128	3,542	3,300
" 27.....	2,573	1,332	1,213	848
June 14.....	2,933	1,473	1,192	515
" 28.....	443	492	925	657
July 9.....	149	225	317	227
" 21.....	102	85	218	178
August 10.....	128	124	258	228

Such are subject to the usual error involved in quantitative sampling of any natural population. These totals, for adult and immature specimens, are the values given in the table and figure. In addition to these, the total number of viable eggs produced just prior to each sampling is given. These are obtained by multiplying the mean number of eggs/adult, for all sizes of adults, times the total number of adults times the percentage of adults with broods showing no degeneration. As some of the broods containing degenerating eggs also contain viable ones, the estimates arrived at in the manner described will be low. However, they will not be much too low as the percentage of these exceptions is small. The fluctuation of the total number of viable eggs is indicated by the solid line.

The dominant maximum of this curve falls on April 29, at the time when there are large numbers of first generation adults present, many of them of very large size, producing large numbers of eggs (see histogram, Fig. 9). All of these eggs will develop into individuals of the second generation which will dominate the population in the following weeks, just as a dominant year-class of fish makes its presence noticeable for several subsequent years. From the middle of May to the middle of June practically all adults belong to the second generation. The small number of viable eggs produced by this tremendous adult population of the second generation is remarkable. The complete and rapid disappear-

ance of this generation in the last half of June can undoubtedly be attributed, in part at least, to the rapid rise in temperature between June 14 and 28. The secondary maximum in the curve for the immature population seen in Figure 10 appears to be comprised of intermediate instars of the third generation. With the warming of the waters these quickly mature and die so that on June 28, the third generation forms a minority whereas two weeks previous there had been twice as many of the third generation, as intermediates, as there had been of the numerous second generation adults. The onset of tachyauxis falls in the same interval which sees this rapid reduction of the population size. It is clear that the number of individuals which possesses tall helmets is almost insignificant beside the horde of predecessors earlier in the season whose helmets were not so remarkable.

#### AN EXPERIMENTAL STUDY OF HELMET FORMATION IN *DAPHNIA RETROCURVA*

The only previous attempt to culture *Daphnia retrocurva* was made by Banta (1939) using helmeted adults from Wisconsin. He found that individuals reared in the laboratory (presumably at 20° C.) did not develop retrocurve helmets as elevated as those of the parent female. The size of helmet attained by the adults of 13 successive laboratory generations derived from this retrocurve-helmeted individual was nearly constant, as judged from his Figs. 144-150.

As we know from our analysis of helmet development in the lake two components affect the final helmet size, the relative size at birth and the rate of subsequent growth. The experiment of Ostwald (1904) indicated that temperature is important in determining the size of the neonate head in *Daphnia cucullata*. Those of Coker & Addlestone (1938) demonstrated that temperature controls the "spike" on the heads of the *Daphnia galeata*. These results as well as the correlation between the relative head length of the neonatae and temperature during the embryonic development of *D. retrocurva* made necessary a close study of the  $\frac{HL}{CL}$  ratio of neonatae which developed at controlled temperatures in this species.

The preceding analysis of post-natal helmet growth in the lake indicated a lack of relation between temperature and relative rate of helmet growth. Experimental confirmation of this point seemed desirable. Because of the lack of correlation between level of nutrition and either phase of helmet formation no experiments testing the effects of quantity of nutrition were performed on *D. retrocurva*. Although there is no evidence, except that which Wolterck reports, that level of nutrition is of primary importance in determining the post-natal relative rate of head growth, a series of helmeted *D. longispina* were reared at different levels of nutrition. The size of the helmets of the adults which developed at all three levels was the same. The results, not given



in detail at this time, will be presented in a later contribution.

Two constant temperature chambers were available. One was maintained at 6°-7° C. the other at 10°-12° C. For higher temperatures two well insulated rooms were used. During the hottest part of the summer one of the rooms was supplied three times a week with ice which kept the temperature near the desired level, although it fluctuated rather freely between 21°-24° C. The two constant temperature chambers and the iced room were each equipped with a 14 watt daylight fluorescent lamp. The other room, used for a short period only, was lighted by the sun.

As culture vessels 500 ml. Erlenmeyer flasks were originally used. However, in later series, it was necessary because of the limitation of space to utilize flasks of 250 and 125 ml. capacity. These flasks were filled to the neck with water in order to reduce the surface area, minimizing the danger of the animals being caught therein. In one experiment the vessel was a museum jar with inside dimensions of 15 x 9 x 7.5 cm. This was used in the un-iced room and the large volume of water (800 ml.) was intended to reduce fluctuation in the water temperature. Water from Bantam Lake, twice filtered through screen silk, was used in all cultures. They were fed a mixture of small green algae with some bacteria. A culture of this algal mixture was maintained in the light by adding from time to time small amounts of a liquid containing some of the readily soluble elements of a commercial fertilizer. A sufficient amount of this food was added to ensure that the animals were well fed.

The females were caught in vertical tows and added to a one gallon jug nearly full of surface water. This was brought back to the laboratory within one to three hours and kept as near to the temperature of the surface water in the lake as possible until the *Daphnia* were isolated in the culture vessels.

In the accompanying Table 13 the experiments are given numbers in parentheses. Experiments (1) through (4) were run in the constant temperature chambers. Number (1) used 500 ml. Erlenmeyer flasks, Nos. 2 and 3 used both 250 and 125 ml. flasks and (4) was in a 125 ml. flask. Experiments (5) through (7) utilized the large museum jar (800 ml. water) in the room lighted only by the sun (southern exposure). Flasks of 125 ml. capacity were used in the remainder and they were kept in the iced room. In all cases the light was considered adequate for the requisite amount of photosynthesis, with O<sub>2</sub> production and CO<sub>2</sub> uptake, by the algae. There were no indications of oxygen lack or CO<sub>2</sub> accumulation and the gas content of the media was not tested.

The effects of population density as revealed in studies on male production (Banta, 1939, and others) and egg production (Pratt, 1943) in *Daphnia* necessitate the consideration of this factor. As critical densities in one race have little or no significance for other races, the only fruitful comparisons can be

made between the population densities in the culture vessels and those found in the lake. The maximum densities attained in the culture vessels were between 3 and 10 animals/100 ml., increasing with the temperature. Estimates of the density in the lake were made in the following manner. The total number of specimens found in the four trap samples taken in the zone of two meters depth supporting the greatest numbers of *Daphnia retrocurva* was divided by the total volume of these samples (40 liters). Some mean density values for the entire lake are also given, although these are probably of less significance. Comparison of the two tables (Tables 11 and 12) shows that the maximum densities encountered in culture vessels at lower temperatures were about the same as those found in the lake from April 29 to June 14.

TABLE 11. Population density of *D. retrocurva* in Bantam Lake, 1945. Values given in animals/100 cc.

	April 29	May 13	May 27	June 14	June 28	July 9
Stratum of 2 meters' depth with population maximum = maximum density	3.81	5.88	5.87	5.52	1.41	0.79
Entire lake = mean density	.....	3.65	.....	.....	0.67	0.34
		Max. pop. size			Max. neonate HL CL	Max. rate post- natal growth

The densities in the cultures at 21°-24° C. were about ten times as great as those in the lake at the same temperature when large helmets were being formed (June 28, July 9).

TABLE 12. *Daphnia retrocurva*. Summary of maximum population densities attained in laboratory cultures.

Experiment Number	Volume of Vessel-ml.	Maximum number present	Maximum population density animals/100 cc.	Temperature °C.
(1).....	500	15	3.0	6 - 7
(2).....	250	8	3.2	6 - 7
(2), (3).....	125	6	4.8	6 - 7
(4).....	500	27	5.4	10 - 12
(5), (6), (7).....	800	30	3.75	14 - 24
(8), (9).....	125	11	8.8	21 - 24
(10), (11).....	125	12	9.6	21 - 24
(12), (13).....	125	10	8.0	21 - 24

#### RELATIVE HEAD LENGTH OF NEONATAE

The results are given in two parts, relative head length in neonatae and post-natal growth. Those pertaining to the former will be discussed first. Table 13 summarizes all of the data. The only consistent correlation which appears is that between temperature during embryonic development and relative head length of neonatae. There is no evidence of pre-

TABLE 13. *Daphnia retrocurva*. Experimental study of relation between HL/CL ratio of neonatae and temperature.

Experiment No	Temperature °C.	Generation of Mother	No. Adults	Total No. Broods	No. Neonatae	Range HL/CL values	Mean HL/CL
(1).....	6 - 7	Overwintered (April 1)	1	1	6 (only 2 measured)	0.488	0.488
(2).....	.....	2nd. gen. (lab.)	4	4	6	0.450 - 0.545	0.510
(3).....	.....	3rd. gen. (lab.)	1	1	2	0.543 - 0.546	0.545
Ceneral Weighted Mean for 6° - 7° C.							0.514
(4).....	10 - 12	Same Ind.	2	2	13	0.500 - 0.558	0.532
(5).....	14 - 17	1st gen.	Sev.	1	4	0.586 - 0.617	0.603
(6).....	17 - 19	(April 29)	"	1	5	0.642 - 0.667	0.652
(7).....	21 - 24	"	"	1	9	0.650 - 0.700	0.667
(8).....	.....	2nd. gen. (lab.)	3	5	11	0.645 - 0.738	0.680
(9).....	.....	3rd. gen. (lab.)	3	3	5	0.590 - 0.667	0.628
(10).....	.....	2nd. gen. (June 14)	2	4	18	0.610 - 0.712	0.643
(11).....	.....	3rd. gen. (lab.)	1	1	2	0.628 - 0.667	0.648
(12).....	.....	3rd. gen. (June 28)	9	9	25	0.630 - 0.762	0.699
eggs laid in lake							
(13).....	.....	Eggs laid in lab.	6	10	22	0.602 - 0.745	0.666
General weighted mean for 21°-24° C.							0.677

induction nor of effect of generation number. In Fig. 7 the relation between temperature and the neonate  $\frac{HL}{CL}$  ratios as indicated by two sources of information is shown. The solid circles represent the experimental findings, at controlled temperature. The crosses represent the relation between the relative head length found in the lake during the course of the season, and the water temperature which prevailed during the embryonic development, as estimated from the curve in Fig. 6. This latter method is crude and the points thus determined are of less significance than those from the experimental study.

The relation between temperature and relative head length at birth appears to be a linear one. There is no evidence for a critical temperature value as Coker & Addlestone assumed for *Daphnia galeata*.

To prove conclusively that temperature during embryonic development is the primary factor determining the  $\frac{HL}{CL}$  ratio in the neonatae, females were kept within a given temperature range while a clutch of eggs was laid and the embryos born, then kept at a different temperature while a subsequent brood developed. The  $\frac{HL}{CL}$  ratios of the neonatae of the two broods can then be compared. Although this procedure sounds simple, *Daphnia* are very susceptible to temperature shocks; the number of successful experiments is small, yet sufficient to demonstrate the relationship.

In experiment 45-17-C. the parent was one of the off-spring of the single *Daphnia retrocurva* female taken alive on April 1. This parent was born and reared at 6°-7° C. When examined on July 11 her CL was 908 micra and there were two embryos in the brood pouch. Her gut was green with algae.

On July 19 the embryos were born. Their  $\frac{HL}{CL}$  ratios were 0.500 and 0.521. These neonatae were removed and the flask with the mother only was transferred

to the 11° C. chamber at 5:30 P.M. At 4:00 P.M. the next day it was changed to the 21°-24° C. room. The mother did not produce any eggs at the molt preceding the transfer but she molted the day after being raised to 21°-24° C. On July 24, four neonatae were found, which had hatched within the 16 hours

previous to measuring. Their  $\frac{HL}{CL}$  ratios ranged from 0.613 to 0.672, with a mean of 0.629. Although the numbers are small the difference between the 0.500-0.521 range at 6°-7° C. and 0.613-0.672 at 21°-24° C. is highly significant. These values are characteristic ones for those temperatures as a glance at Table 13 will show. The mother and neonatae produced at the two temperatures can be seen in Fig. 11.

The females used in the second experiment were caught on April 29. They belonged to the second generation of the season. Two of these were kept at 10°-12° C. as controls (Exp. No. 4, Table 13) and the others were kept at room temperatures in a single vessel. (Exp. Nos. 5-7, Table 13.) As there was no apparatus available for maintaining constant high temperatures at various levels, it was necessary to keep the cultures in a large well insulated room where temperature changes were slow. By measuring the water temperature daily, the effective range for the 3 or 4 days prior to birth could be found. The volume of water used (800 ml.) tended to minimize temperature fluctuations.

The results of this experiment are given in the previous table (13), for temperatures 14°-17° C., 17°-19° C. and the first line of the 21°-24° C. group.

The range of  $\frac{HL}{CL}$  values at 17°-19° C. was well above the 14°-17° C. range, but overlapped that of the higher range. The values for the controls at 10°-12° C. were below those found for 14°-17° C.

These two experiments conclusively show that temperature is the primary factor controlling the relative length of the neonate head in *D. retrocurva*.

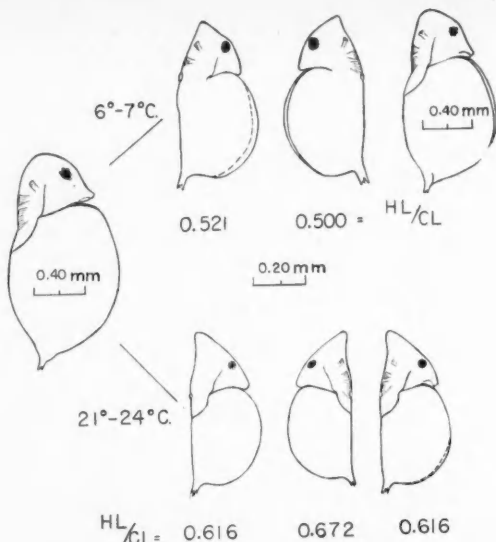


FIG. 11. *Daphnia retrocurva*, 1945. Camera lucida drawings showing neonatae of two successive broods of the same female. One brood was reared in the laboratory at 6°-7° C., the following one at 21°-24° C. The neonatae are all drawn at the same magnification. An adult which developed at 6°-7° C., not from either of the neonatae delineated but from a similar one, is drawn at the same magnification as the mother. This adult is to be compared with that of the same size in Fig. 14, which developed at 10°-12° C.

#### POST-NATAL GROWTH

The most striking feature of the post-natal development of *D. retrocurva* in laboratory cultures is that the relative growth of the helmet is always bradyauxetic. This is readily apparent in Fig. 12.

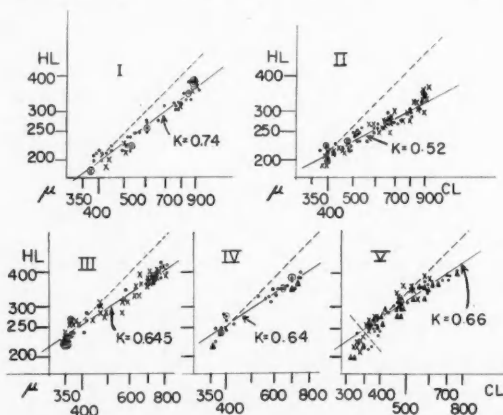


FIG. 12. *Daphnia retrocurva*, 1945. Graphs of the HL and CL of *Daphnia* reared in the laboratory. Stock derived from Bantam Lake, 1945. The pecked line has a slope of 1.0 making evident the bradyauxetic nature of post-natal helmet growth in the laboratory. Lines of best fit drawn by sight. Symbols are encircled when more than one neonatae have the same measurements.

GRAPH I. Descendents, born and reared at 6°-7° C., of an overwintered female collected on April 1. Crosses represent first generation offspring; dots the second.

GRAPH II. Offspring, born and reared at 10°-12° C., of two adults of the first generation taken from Bantam Lake on April 29. Crosses represent offspring of one female; dots the other.

GRAPH III. Descendents of an adult of the first generation which was taken on April 29. These were born and reared at 21°-24° C. Crosses represent her offspring (i.e. 2nd generation) and dots the 3rd generation.

GRAPH IV. Descendents of a second generation female taken on June 14. These were born and reared at 21°-24° C. Crosses represent her offspring (3rd generation) and dots the 4th generation. The triangles are successive measurements of a single individual developed from an egg present in the brood-pouch of the original female when taken in the lake.

GRAPH V. Offspring of three females (3rd or 4th generation) taken on June 28, after tachyauetic growth had begun in lake. These offspring (4th or 5th generation) were born and reared at 21°-24° C. Different symbols are used for the offspring of each female.

Here the pecked line represents isauxetic helmet growth from the mean neonata. The points and the solid line drawn by sight through them all fall short of isauxesis. This constant discrepancy between development in the laboratory and in the lake is in sharp contrast to the reproducibility in culture of the neonate  $\frac{HL}{CL}$  variations found under natural

conditions. The cause of this bradyauxesis in the laboratory is completely unknown. Several factors can be eliminated from the field of possible causes. On the quantitative side nutrition in the laboratory was ample, surpassing that found in the lake during most of the period investigated. It will be remembered that in the lake nutrition approached adequacy only during April and the first half of May. The possibility exists that some qualitative difference between the lake algae utilized as food and those furnished in the laboratory cultures may be involved. The probability of such a difference being of importance is small. Berg (1936) found that in *D. cucullata* the lake algae could be replaced by other green algae and permit tachyauetic post-natal growth in the laboratory. The difference between the 6°-7° C. and 10°-12° C. cultures cannot be a question of generation number, since the individuals of both belong to the second generation of the season. It is also quite apparent that generation number makes no difference in the relative growth rate at 21°-24° C. for individuals of different generations show the same degree of bradyauxesis.

Although the differences between the rates of relative helmet growth in the lake and in the laboratory appear at present to be correlated only with the presence of the *Daphnia* in the lake or the laboratory, there are differences in the degree of bradyauxesis in culture which vary with the temperature. However, the relation is not a simple one. The minimum rate of relative helmet growth occurs at 10°-12° C.,  $k = 0.52$ , while at 6°-7° C.,  $k = 0.74$  and at 21°-24° C.,  $k$  values from 0.57 to 0.66 have been found. (Fig. 12.) The result of growth at the minimum relative rate can be seen by comparing the adult

figured at the right end of the upper line in Fig. 13 with that in a similar position in Fig. 11. The adult in Fig. 11 did not develop from either of the neonatae figured but from a similar one born and reared at 6°-7° C. It is a typical specimen. Comparison of the two adults (each has CL = 865 micra) shows that the one reared at 6°-7° C. has a taller helmet than that reared at 11° C., although the latter had a higher  $\frac{HL}{CL}$  ratio at birth. This peculiar relation to temperature suggests that more than one physiological processes are involved in post-natal relative helmet growth in the laboratory.

It is of interest to speculate on the possible relation which exists between the various factors involved in the control of post-natal helmet growth. The factors in the lake cause isauxetic growth at all temperatures below ca. 19° C. and allow varying degrees of tachyauexis above it. In the laboratory all head growth is bradyauxetic. This indicates that at least one factor present in the laboratory depresses relative growth. This factor, which apparently has a positive temperature characteristic, must act in conjunction with another, which has much the same effect upon relative growth that the lake factor does, to give the observed relation between temperature and degree of bradyauexis. It is reasonable to suppose that the lake factor is identical with this one of the factors active in the laboratory. That having a depressant effect appears to be peculiar to the conditions of laboratory culture. However, there is some indication in the observations of Wesenberg-Lund (1908) that bradyauxetic helmet growth occurs in *D. cucullata* in the fall and winter. As the samples of *D. retrocurva* did not extend into the fall it is not known whether bradyauexis ever occurs in this species under natural conditions.

It seems desirable to review at this point Banta's (1939) "regression" of the helmets of adults from the lake after they have been in laboratory culture. His one case of extreme "regression" is based upon an individual which had failed to cast its head casque. The much smaller new helmet could be seen within the old (his Fig. 143, p. 239). In no instance was anything resembling this found in our cultures, and it seems likely that this specimen was abnormal. In addition Banta says "the drawing was hastily made and is not highly accurate." The history of one other individual is given as showing less "regression" than the above abnormal specimen (his Figs. 151, 152, p. 239). Banta's criterion of "regression" was the decrease in the curvature of the dorsal margin of the head. This is due not to a regression in length, but to a greater rate of increase of the dorso-ventral breadth of the base of the head than of the length of the head. This same type of alteration of the shape of the helmet was evident in adults of the Bantam *D. retrocurva* as they aged in the lake (Figs. 4 and 5); more so after being brought into the laboratory. The observation that adults of succeeding parthenogenetic generations all had simi-

lar helmets, much smaller than that of the original female, was the basis of Banta's statement that,

At least most of the regression occurred within a single generation. (1939, p. 238, l. 9.)

This conveys a misconception of the process involved. As all the offspring were reared in the laboratory, at about 20° C., the post-natal helmet growth of all must have been similarly bradyauxetic. Generation number is of no consequence in helmet growth of this species. The laboratory adults derived from *D. retrocurva* of Wisconsin, seen in Banta's Figs. 144-150 are nearly identical to those developed at a similar temperature from specimens of Bantam Lake, Conn., Figure 13.

One phase of the results of the laboratory cultures remains to be mentioned. This is the appearance of the neonatae produced in culture at temperatures of 21°-24° C. As can be seen in Graph V of Fig. 12, most, possibly all, of the young born are smaller than the neonatae produced by the same mothers when a large part of the period of development was passed in the lake. These smaller neonatae also have relatively smaller helmets than normal sized ones do. As these smaller neonatae only occur in cultures at high temperatures it is assumed that the temperature is responsible for these premature births. Higher temperatures appear to shorten the length of the adult instars so that the embryos escape from the brood pouch before attaining that stage of development usually reached at the time of birth at lower temperatures. The embryos in the brood pouch are apparently capable of independent existence for some hours before they are usually released. That these premature neonatae should have relatively shorter helmets is noteworthy. It indicates that just prior to hatching the relative rate of helmet growth is high. Observation of developing embryos confirms this. In two of the 21°-24° C. cultures it was possible to compare the post-natal development of a brood of these premature forms, with a previous brood whose neonatae were of normal size. In graph I of Figure 14 the crosses represent dimensions of successive instars of an individual which developed partially in the lake while the dots represent successive measurements of two individuals which constituted a brood whose entire embryonic development was passed at higher laboratory temperatures (and released prematurely). A line drawn by sight through the crosses gives  $k = 0.57$ . The helmets of the premature individuals showed a relatively high rate of increase until they reached the size of normal neonatae. Thereafter helmet growth was bradyauxetic, and although the subsequent history was not followed the indications are that the  $k$  value is exactly the same as for the previous brood. Graph II of the same figure represents two broods of two individuals each. The symbols have the same meaning as before. The relative growth rate of the helmet in the first brood, as measured by a line of sight, corresponds to a  $k$  of 0.575. The helmets of the premature neonatae did not develop at the same

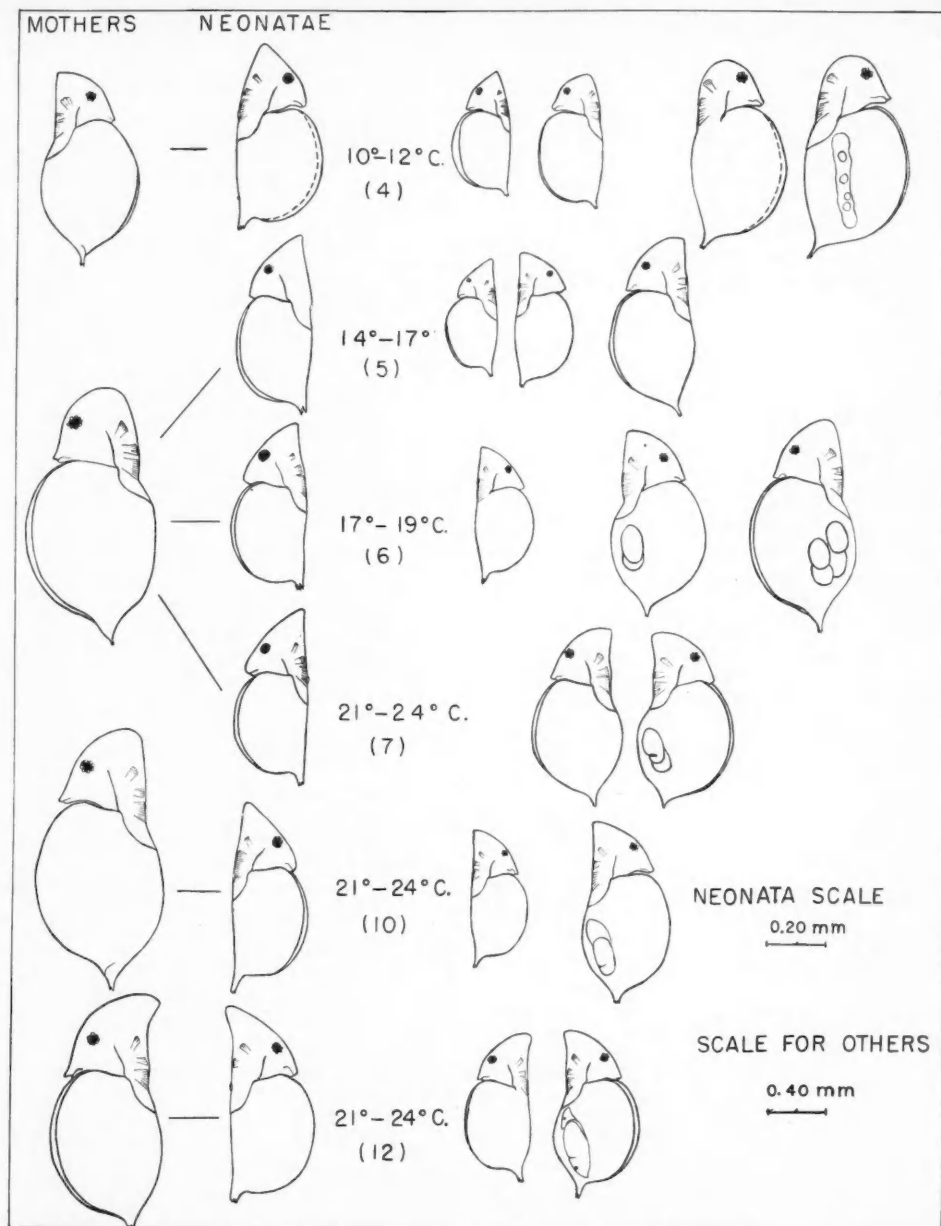


FIG. 13. *Daphnia retrocurva*, 1945. Camera lucida drawings illustrating post-natal growth at different temperatures in laboratory cultures. The numbers in parentheses refer to the experiment numbers in Table 13.

high relative rate as in the previous case. Here  $k = 1.025$ , higher than the  $k$  characteristic of subsequent growth at that temperature. This case does not have as many measurements as the previous one. Graph V of Figure 12 shows that a high rate of relative helmet growth in premature neonatae, with  $k$  more nearly equal to 1.25 rather than 1.025, is more common in the cultures. This is very sugges-

tive since the  $k$  value for relative helmet growth in the lake on June 28 was about 1.25; the tachyauetic growth rate in the lake after birth may be a continuation of the high relative growth rate which obtained just prior to birth. Although this phenomenon of premature birth is most evident in the offspring of females taken from the lake on June 28 when post-natal helmet growth was tachyauetic



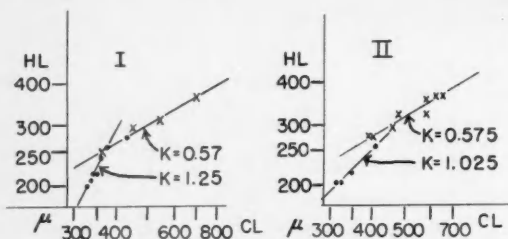


FIG. 14. *Daphnia retrocurva*, 1945. Premature births at high temperatures in laboratory culture. See text for explanation of symbols.

(Graph V), it appears to be present, to a more limited extent in the descendants, reared at high temperatures, of a female taken on April 29.

#### SUMMARY OF FINDINGS FROM LABORATORY CULTURE OF *Daphnia retrocurva*

1. The relative neonatae head length is determined primarily by temperature. The relationship is a linear one, with no indication of a critical temperature. All generations appear to be equally competent to produce neonate helmets of the maximum relative size.

2. Relative growth of the helmet during post-natal development is bradyauxetic in laboratory cultures.

3. The degree of bradyauxesis in laboratory culture varies with the temperature, and has its lowest value at an intermediate temperature (10°-12° C.). This suggests that the relative rate of helmet growth under laboratory conditions is influenced by two sets of conditions with opposing effects.

4. The correlation between the maximum  $\frac{HL}{CL}$  ratio of neonatae and tachyauuxesis, apparent in the analysis of the seasonal development of cyclomorphosis, is not found in the laboratory cultures. Both of these phenomena are restricted to high temperatures (19°-24° C.). This high temperature is the primary factor producing neonate helmets of the maximum relative size, while the factor(s) producing tachyauuxetic helmet growth operate only at these higher temperatures.

5. Measurements of certain small and apparently prematurely hatched neonatae suggest that the mechanism of tachyauuxetic growth during the post-natal period may be a continuation of the high relative rate of helmet growth during the last period of embryonic life.

#### A STUDY OF THE ALTERATION OF THE HEAD SHAPE OF *DAPHNIA GALEATA*

Of the two groups of investigators (Banta, Coker & Addlestone) who have published results of laboratory studies on the modification of head form in this species, those of Coker & Addlestone (1938) are more significant. They used a race from University Lake, Chapel Hill, N. C. individuals of which have strongly pointed heads in late spring

and early summer. When eggs of this population develop below 11° C. the heads of neonatae are always rounded, while above 15° C. all the newborn have spiked heads. At intermediate temperatures the neonatae may or may not be spiked and when a spike is present, it is small. Practically all of these spiked neonatae lost these spikes in the course of the first few molts. The only exceptions were some animals reared at 11° and 15° C. in containers larger than shell vials (size not specified) in which a vestige of the spike at least persisted throughout life.

The findings of Banta (1939) on the behavior of the spike in two populations of *D. galeata* are consistent with these results. The animals came from a pond near Cold Spring Harbor, Long Island, N. Y., and from Lake Okeechobee, Florida. The young of both populations born in laboratory cultures, ca. 20° C., always bore spikes, which they subsequently lost. Banta names the two races with which he worked *Daphnia pulex* form *galeata* and cites Birge (1918) as the authority. However, Birge (1918) gives a *galeata* type of *D. longispina* but not of *D. pulex*. As Banta also refers to the *mendotae* form of *Daphnia pulex*, when he undoubtedly means *D. longispina* form *mendotae* Birge, 1918, it appears that the species name *pulex* has been erroneously used twice for *longispina*. If these forms do have a distal pecten on the post-abdominal claw, which would place them in *D. pulex*, this will be one more piece of evidence that these two species, as defined, are not valid. Only examination of specimens can settle this point.

The desire to confirm the findings of Coker & Addlestone on the effects of temperature in *D. galeata* was heightened when hypolimnetic populations belonging to this species were found in two Connecticut lakes (Highland and Shenipsit) bearing spikes at temperatures of 7°-8° C. At this temperature the Chapel Hill race would have lacked spikes. Although attempts to get some of the Shenipsit population into culture were unsuccessful, success was met with a morphologically similar population occurring in Bantam Lake.

The population of spike-headed *Daphnia galeata* used in this study was one of the four races of *Daphnia* which lived in Bantam Lake during 1945. This material was subjected to the treatment outlined for *Daphnia retrocurva*. The only deviation was in the manner of measuring HL. With heads of this shape HL is simply and satisfactorily measured with the ocular micrometer as the straight line distance along the long axis of the body between the base of the head (as in *D. retrocurva*, cf. Fig. 2) and its anteriormost point. An attempt was made to measure the length of the spike. This is neatly done when the spike is small. The large ones merge so imperceptibly into the altered outline of the head that division of the spike from the rest of the head becomes very arbitrary, and the resulting values for length of spike are highly variable. Due to the small number of values and their great variability,

their significance is doubtful and no detailed remarks will be made thereon. At a later point the relationship of the "spiked" head shape to head length will be discussed.

The notes on the methods of culture of *Daphnia retrocurva* apply as well to *Daphnia galeata*.

#### RELATIVE HEAD LENGTH OF NEONATAE

As in the case of the previous species discussion of the cyclomorphosis will be divided into its two aspects, relative head length at birth and post-natal relative growth. Data concerning the first of these can be derived from two sources, plankton catches and laboratory culture.

All of the information concerning the relative head length of neonatae taken at intervals throughout the season, and the corresponding temperatures, is presented in Table 14. As the adults are found in different strata at different times of the season, the range of their vertical distribution is given. These are based upon midday series. Unfortunately nothing is known of the diurnal vertical migration of this population. Very similar populations of spiked *D. galeata* occur in at least two other lakes of Connecticut where their vertical movements in midsummer are known. During thermal stratifications these populations are restricted to the hypolimnion both day and night. This situation is very like that found by Kikuchi (1930) in two Japanese lakes in which the populations were restricted both day and night to the hypolimnion during summer stratification. The temperature range of the strata inhabited by the adults in Bantam Lake during the day is taken as the range to which the embryos are subjected during development. The estimated temperatures for a

period of several days before the sampling dates are given. The mean values for the relative head length of the neonatae born in the lake are related to the median temperature estimated to prevail during the period of development by the crosses of Fig. 15.

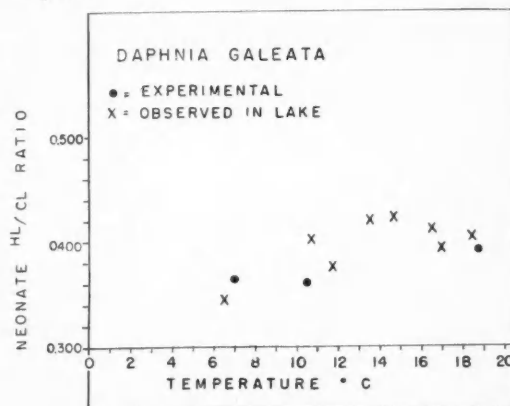


FIG. 15. *Daphnia galeata*, Bantam Lake, 1945. Table of correlation between neonate HL/CL ratio and temperature during embryonic development. Data for lake temperatures given in Table 14.

Although there are fewer laboratory cultures of this population of *galeata* than of the *retrocurva* previously considered, they are sufficient to shed some light upon the relationship between temperature and relative neonate head length. This information is summarized in Table 15. Males and sexual females of *Daphnia galeata* often appeared in laboratory cultures, a complication which never occurred

TABLE 14. *Daphnia galeata*. Relation between temperature and neonate HL/CL in Bantam Lake, 1945.

Date	Vertical Distribution		Estimated Temp. Range during emb. dev.	Neonate HL/CL Range	Mean Neonate HL/CL	Mean HL (Micrometer Units)	Mean CL (Micrometer Units)	Number Neonatae
	Adults	Temp. °C.						
April 1.....	2-4 M	0M= 8.2 7M= 8.2	5° - 8° C.	0.326 - .355	0.345	16	46.3	7
" 15.....	3-6 M	0M=14.1 6M=14.1	12° - 14° C.	0.362 - .468	0.420	19.4	46.2	8
" 29.....	1-7 M	0M=12.0 6.5M=11.1	11° - 12.5° C.	0.340 - .403	0.376	17.7	47.1	8
May 13.....	1-6 M	0M=11.6 6M=11.2	10.5° - 11° C.	0.370 - .456	0.403	19.6	48.7	8
" 27.....	1-7 M	0M=16.8 7M=14.6	14° - 16.5° C.	0.412 - .442	0.427	19.5	45.7	3
June 14.....	2-7 M	0M=22.8 3M=18.2 6M=16.4	15° - 18° C.	0.413	0.413	19	46	1
" 28.....	3-7 M	0M=22.1 7M=16.4	16° - 18° C.	0.396	0.396	19	48	1
July 9.....	6-7 M	0M=24.2 7M=18.1	18° - 19° C.	0.405	0.405	17	42	1

TABLE 15. *Daphnia galeata*. Relation between neonate HL/CL ratio, spike development and temperature in laboratory cultures.

Mother Number	Temp. °C. Range	Neonate HL/CL Range	Mean HL/CL	Mean HL (Micrometer Units)	Mean CL (Micrometer Units)	Number Neonate	Spike
45-3.....	6.8-7.2	0.334-.357	0.345	14.5	42	2 meas. ♂♂ (brood of 15)	+
	10-11	0.347-.380	0.361	16.9	46.9	6 ♀♀	+, ++
45-4.....	6.8-7.2	0.348-.395	0.367	16.4	44.8	15 ♀♀	±
45-4.....	3-7	0.314-.347	0.328	16.4	48.7	7(3♂♂)	—
45-7.....	10-12	0.308-.326	0.317	16.0	50.5	2♂♂	+
RT.....	18.5-19	0.370-.400	0.391	17.8	45.7	6♂♂	++++, +++++

with *D. retrocurva*. The single culture at 18.5°-19° C. produced males, for which the value of the neonate  $\frac{HL}{CL}$  ratio may be slightly lower than it would be for parthenogenetic females. However, to judge from the second brood of female 45-4, which consisted of 3 males and 4 females, the difference in  $\frac{HL}{CL}$  ratio in neonatae of the two sexes is small (mean = 0.326 for the males, 0.330 for females). With the exception of this second brood of female 45-4, excluded because the temperature range was too great, the mean  $\frac{HL}{CL}$  ratios for neonate of the laboratory cultures are plotted against the median values at the three temperature ranges as dots in Fig. 15. It will be noted that the weighted mean of HL/CL for 6.8°-7.2° C. is 0.364, while that for 18.5°-19.0° C. is 0.391.

It appears from Fig. 15 that there is a continuous relation between temperature and relative neonate head length. The small difference between the relative neonate head lengths at low and high temperature, however, does not give a clear conception of the differences in shape. It will be noted in Fig. 16 that there is no close correlation between  $\frac{HL}{CL}$  ratio of the neonatae and the size of the spike. The spike is not to be conceived as an additional piece stuck onto the anterior end of the rounded head of low temperatures, but rather as formed by a reshaping of the material of the round head. Since, as noted previously, measuring spike length accurately is not feasible, an attempt at a quantitative comparison of spike sizes at different temperatures is made in Table 16. The degrees of alteration of the head shape from the completely rounded to the maximum degree of pointedness (seen in the neonatae collected June 14 and 28), are designated by a series of symbols; (—) indicates a round head, (+) the presence of a small spike, . . . . . (+++++) the maximum development of the spike. The neonatae in Figure 16 are classified by way of illustration. The correlation between temperature and degree of alteration appears more consistent than does that between temperature and  $\frac{HL}{CL}$  of neonatae. The temperature

at which spikes make their appearance is 7° C. The spikes, somewhat smaller than the maximum size, produced above 17° C. may represent a true decrease due to the general deleterious effect of such high temperatures on this race of *D. galeata*.

TABLE 16. *Daphnia galeata*. Relation of temperature to head shape in neonatae. The degrees of alteration of the head shape represented by the symbols are best seen in Figure 17.

Temp. Range °C.	Degree of Alteration of Head Shape	
	Lake	Lab. Culture
3-7.....	—	—
5-8.....	—	—
6.8-7.2.....	—	+, ±
10-12.....	+++	+, ++
12-14.....	+++++	—
14-16.5.....	+++++	—
15-18.....	+++++	++++, +++++
18-19.....	++++	—

Small populations of *D. galeata* were found, as noted above, in the hypolimnions of two stratified lakes, dwelling in strata where the temperature was between 7° and 8° C. Individuals of both had spiked heads, neonatae as well as all older stages.

#### POST-NATAL GROWTH

The type of relative growth analysis used for *D. retrocurva* was applied here, Figure 17. The points in the April 1 graph fall along a straight line with a slope of 0.64. As the *Daphnia* represented by these points were all born with rounded heads, it was considered that this might be a basic relative growth relation. Lines with this slope drawn through the mean neonatae closely approximate the relative growth rates for the next two months (April 1 through May 27). On June 14, however, most of the points are above the line with a slope of 0.64. A line drawn by sight through them has a slope of 0.80. The 3 specimens of June 28, drawn on the June 14 graph fall on or above this line, while the six of July 9 are nearer to the line with a slope of 0.64. The line with a slope of 0.80 has been added to the May 27 graph for comparison.

The changes in the relative growth rate of the head are interpreted in the following manner. Dur-

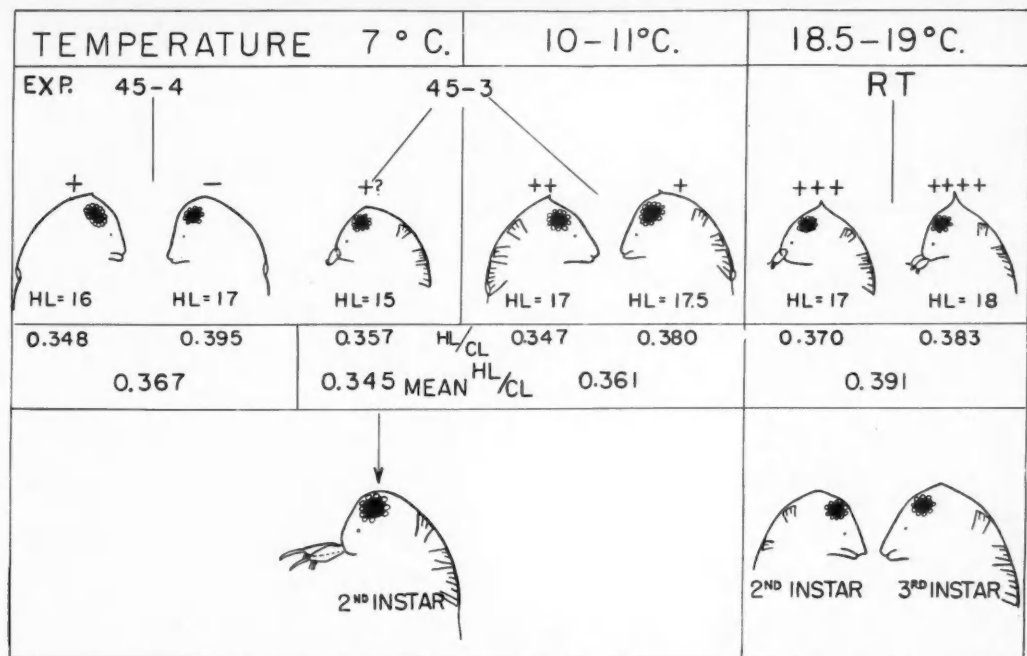


FIG. 16. *Daphnia galeata*, Bantam Lake, 1945. Camera lucida drawings of neonate heads showing lack of correlation between degree of spike development and either absolute or relative head length. The mean HL/CL ratios apply to the broods of the depicted neonatae. Absolute head length expressed in micrometer units (1 m.u. = 8.65 micra). Experiment designations refer to Table 15. Neonatae born in laboratory at temperatures indicated. The loss of the spike after the first molt is demonstrated in the lower panel.

ing the period from April 1 to about May 27 the post-natal growth of the head showed the same degree of bradyauxesis with respect to the carapace, regardless of the shape of the neonate head (rounded, as on April 1, or well spiked, as on April 15). On April 15 the degree of alteration of the neonate head was not as great as it was on June 14 and 28, at which time the extreme was attained. There is some indication that on May 27 a small portion of the population showed an increased rate of relative head growth. On June 14 and 28, HL during post-natal life increased relatively more rapidly than at other times, although the relation was still one of bradyauxesis. On these dates the points are fitted by a line with a slope of ca. 0.80. On July 9 the rate of post-natal relative growth had decreased very nearly to what might be considered the basic relationship, indicated by a line with slope 0.64. It is worth noting in this connection that the rate of relative head growth in the roundheaded *Daphnia pulex* and *longispina* characteristic of ponds is bradyauxetic. Anderson, Lumer & Zupancic (1937) published measurements of a pond-dwelling population of *Daphnia pulex*. From these it was calculated the rate of relative increase in head length corresponds to a  $k$  of 0.67. In a pond population of *D. longispina* from near Mt. Carmel, in Hamden, Conn.,

the relative rate of growth corresponded to a  $k$  of 0.79 (unpublished data of author).

Little can be said concerning the post-natal development in laboratory cultures of the race of *D. galeata* from Bantam Lake. The relative growth rate appears to be about 0.64 although the numbers involved are insufficient to warrant a more definite statement. The one culture in which post-natal growth was followed to maturity (45-7 at 10° to 12° C.) had spike-headed neonatae, but all subsequent instars were roundheads. This loss of the spike is similar to that of the population studied by Coker & Addlestone. Fig. 18 shows the degree of spike development at different times of the season.

#### SUMMARY OF CYCLOMORPHOSIS OF *Daphnia galeata*

1. Neonatae of the Bantam Lake population which develop above 7° C. have spike heads, those below do not.
2. Hypolimnetic populations of *D. galeata* in Highland and Shenispit Lakes are spike-headed at temperatures between 7°-8° C.
3. The degree to which the shape of the head is altered from the roundheaded condition increases with increasing temperature.
4. This transition from round to spiked heads is not due to an increase in the  $\frac{HL}{CL}$  ratio of the

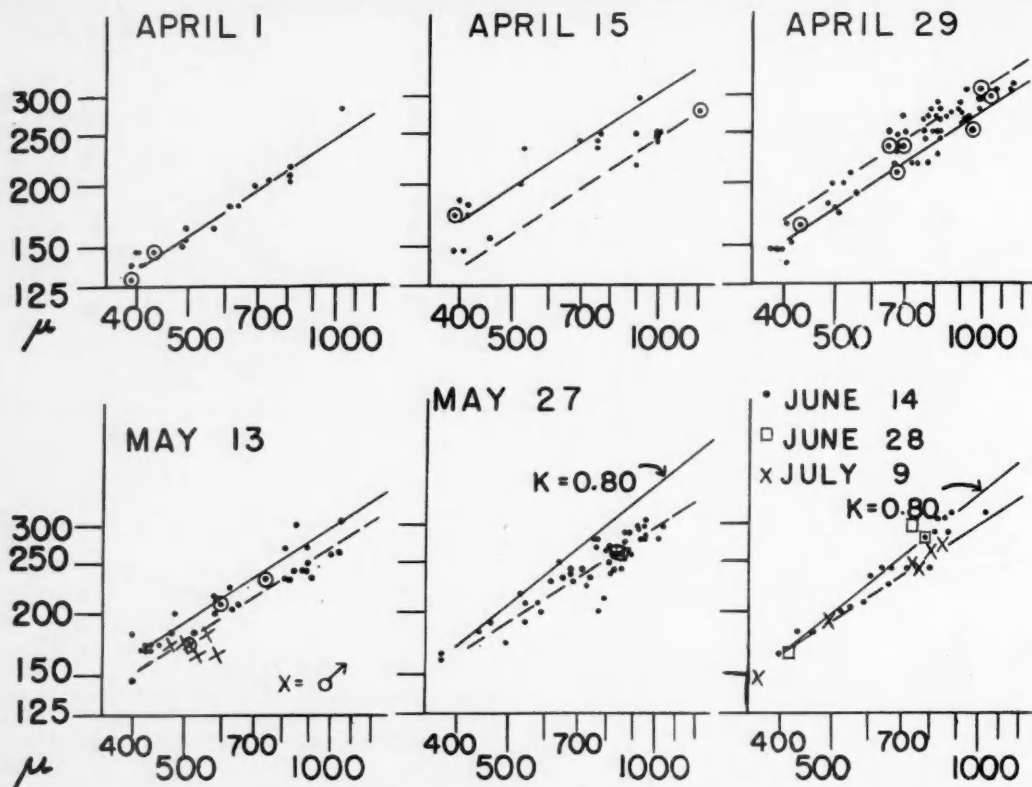


FIG. 17. *Daphnia galeata*, Bantam Lake, 1945. Graphs of relation between the logarithms of HL and CL. The solid lines of the first four graphs are drawn with a slope of 0.64. The points of the June 14 and 28 samples fall along a line of sight with a slope of 0.80. A solid line with this slope is drawn on the May 27 graph for comparison; a solid line with a slope of 0.64 is drawn on the last graph for the same purpose. The solid line for each sample is drawn through the mean neonata. The pecked line on any graph represents the solid line of the preceding one. Encircled points indicate that two specimens have the same measurements.

neonatae, but is a re-shaping of the head. Heads with well-formed spikes as well as those without any trace of a spike may have the same absolute and relative length.

5. The rate of relative head growth in the lake was bradyauxetic, corresponding to a  $k$  value of 0.64 for the early part of the season.

6. For a short period in midsummer the head showed an increased relative growth rate,  $k$  about 0.80.

7. In Bantam Lake all individuals born with spikes retained at least some vestige thereof throughout life. During this period the lake temperature was always above  $11^{\circ}\text{C}$ .

8. The hypolimnetic races in Highland and Shenipsit retained their spikes although the temperature was only between  $7^{\circ}\text{C}$ - $8^{\circ}\text{C}$ .

9. In the laboratory all of the small number of individuals examined lost their spikes after the first or second instar, although the rate of relative increase in HL appeared to approximate the basal rate ( $k = 0.64$ ) found in the lake.

#### COMPARISON OF THE BANTAM LAKE (CONN.) RACE WITH THAT OF UNIVERSITY LAKE (N. C.) STUDIED BY COKER & ADDLESTONE

1. Under natural conditions the North Carolina race can produce relatively larger helmets in adults than have been seen in the Bantam Lake race.

2. Both races become very scarce in midsummer, and usually produce males and sexual eggs just beforehand.

3. Neonatae of the North Carolina race are always roundheaded when they develop at temperatures of  $11^{\circ}\text{C}$ . or less. Those which develop between  $11^{\circ}$  and  $15^{\circ}\text{C}$ . may be either roundheaded or spiked. Above  $15^{\circ}\text{C}$ . spikes are always present.

4. Neonatae of the Bantam race which develop below  $7^{\circ}\text{C}$ . are roundheaded. Those which develop at about  $7^{\circ}\text{C}$ . may be either spiked or rounded. Above  $7^{\circ}\text{C}$ . all neonatae bear spikes.

5. Populations of *Daphnia galeata* which dwell in the hypolimnions of two other Connecticut lakes (Highland, Shenipsit) produced neonatae at  $7^{\circ}$ - $8^{\circ}\text{C}$ . which were spiked. It is presumed that these



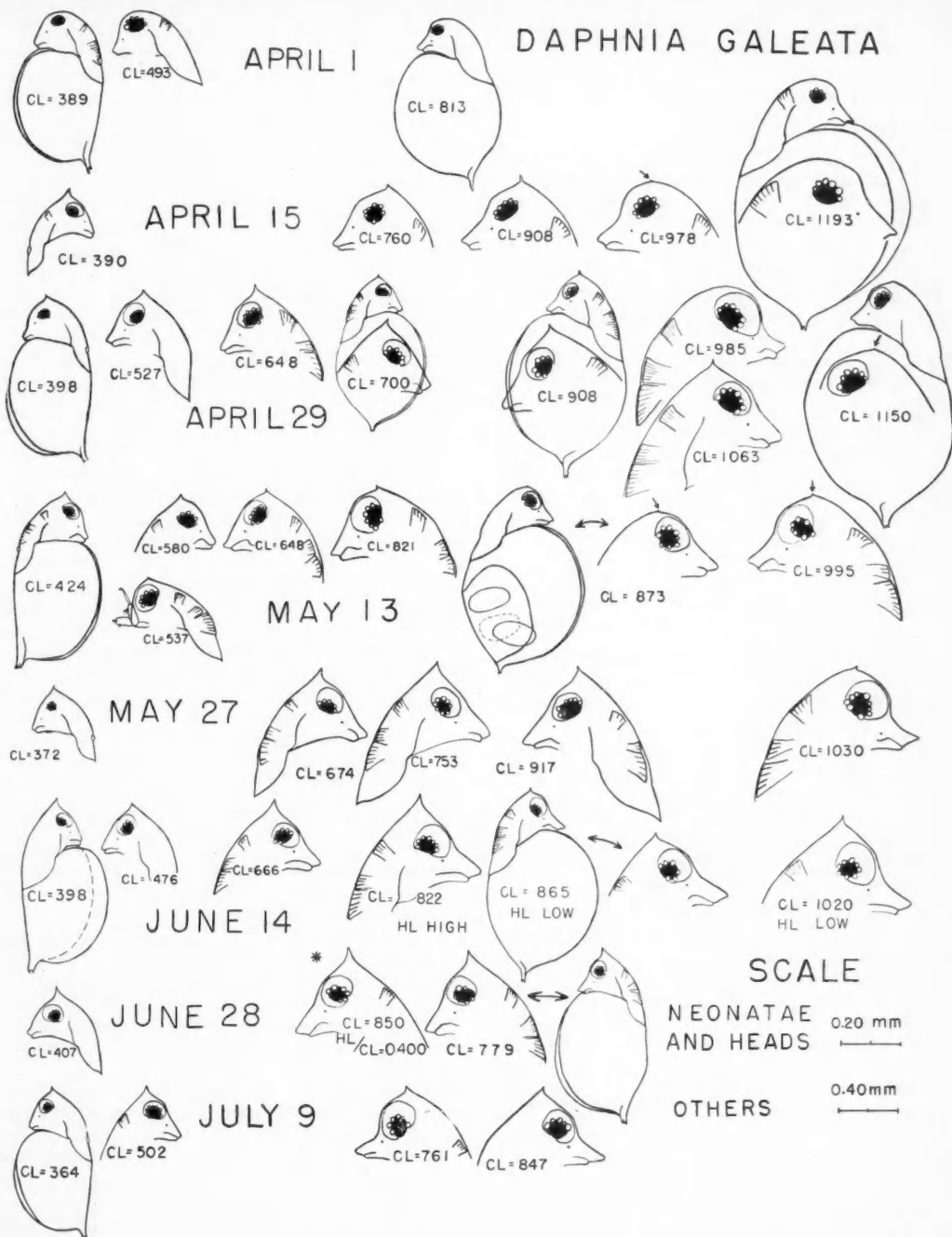


FIG. 18. Camera lucida drawings of *Daphnia galeata* from Bantam Lake, 1945. The degree of spike development is emphasized. The adult with the highest HL/CL is marked with an asterisk. Note sexual female and young male present on May 13.

belong to the same race as the Bantam Lake population.

6. The North Carolina and Connecticut races are alike in that the spike on the head of neonatae reared in laboratory cultures is lost after the first few molts.

#### COMPARISON OF CYCLES OF *D. retrocurva* AND *D. galeata*

The similarity between the sequence of events in *D. galeata* and that found in *D. retrocurva* is remarkable.

1. In each the shape of the neonate head depends primarily upon the temperature during embryonic development. The size as well as the shape of the head of *D. retrocurva* neonatae changes markedly, while in *D. galeata* the alteration of the shape does not appreciably affect the size. (It would be exceedingly laborious to obtain evidence for a more exact statement about the size differences corresponding to different neonata head shapes in this species). In the Bantam Lake population on April 1, 1945 there were neonatae of *D. retrocurva* whose heads were of different shapes but of the same relative length. The two neonatae drawn for this date in Figure 4 illustrate this difference in shape.

2. During the early part of the season the rate of relative growth of the head remains constant, although the shape (and relative size in *D. retrocurva*) of the neonate head is changing.

3. An increase in the rate of post-natal relative growth of the head accompanies the attainment of the maximum degree of modification of the neonate head. It must not be inferred, however, that this is a causal relationship; it is more likely that both occur only at higher temperatures. This stage in the cycle of events is not reached simultaneously in the two species in the same lake, which is at variance with the contention of Wesenberg-Lund that seasonal variation begins at the same time in all cladocera of a lake (1908, p. 246).

4. After a short period (ca. 6 weeks in *retrocurva*, ca. 4 weeks in *galeata*) the relative growth rate of the head decreases to very nearly its level during the early part of the season.

The differences between the cyclomorphoses of these two species are quantitative. The only possible exception, as mentioned above, is the size factor in the alteration of the neonate head.

Further, a comparison between the two species with regard to the differences between growth in the laboratory and the lake is interesting. In both, the shapes and relative sizes of the neonate head found in the lake can be reproduced in laboratory culture (since temperature is the primary controlling factor). But post-natal growth of the head of both species when cultured in the laboratory differed markedly from even the basal growth relations which obtained in the lake during the early part of the season (isauxis in *retrocurva*; bradyauxis with retention of spiked condition in *galeata*).

## DISCUSSION

It was considered, as indicated in the introductory section, that one of the first aims in a re-investigation of the problem of cyclomorphosis must be to ascertain which of the two opposing schools of thought on the causes of this phenomenon is more nearly correct. Woltereck held, apparently on the basis of experimental studies, that the growth of the head is controlled by the nutritive level. Wesenberg-Lund contended from careful observations that growth is controlled by temperature. Those experiments previously performed by Ostwald had indicated that temperature did control the embryonic phase of helmet growth. The first step in the resolution of these differences was taken by Coker & Addlestone in 1938. Working on a form of *Daphnia* with a mild type of cyclomorphosis, they were able to prove that temperature affected the embryonic processes of head formation. Nutrition of the mother had no influence thereon. This evidence that temperature was more important than nutrition in controlling helmet formation threw their weight on the side of Ostwald and Wesenberg-Lund. Post-embryonic helmet growth in well fed animals in the laboratory was different from that in the lake at the same temperature. The discovery of this difference under similar conditions of high temperature and good nutrition is also directly opposed to Woltereck's reports in which he was able in laboratory culture to equal and even improve upon the growth found in nature by maintaining a high level of nutrition (which involved high temperatures). Throughout all of this controversy, which is merely sketched here, it had been considered that all phases of helmet growth were controlled by a single set of environmental factors. Coker & Addlestone furnished evidence that this might not be so. It is now clear, as a result of the present investigation, that the embryonic and postembryonic phases of helmet growth are under the control of different environmental factors. Further discussion must proceed in the light of this new information.

The present researches have shown that in the highly cyclomorphic *Daphnia retrocurva* the embryonic phase of helmet growth, measured by the relative head length of the neonatae, is primarily controlled by temperature. Furthermore the relation between relative neonate head length and temperature is a linear one. Coker & Addlestone's belief that there is a critical temperature for the embryonic phase of helmet formation is possibly due to the small magnitude of the morphological changes in the mildly cyclomorphic form with which they worked. Our investigations on *D. galeata* (to which their spike-headed forms are assigned) indicate that an arbitrary number expressing both the percentage of the off-spring having spike-heads and the degree of alteration of the head shape toward the pointed condition should probably be used as an index of morphological change, rather than a length measurement alone. The relation of this index to temperature would be more nearly linear, with pos-

sibly a minimum temperature below which there is no further morphological change. The following two conclusions can in the present state of our knowledge, be drawn:

1. In the *pulex-longispina* species group the embryonic phase of helmet formation is primarily and directly controlled by temperature.

2. The degree to which this process of embryonic helmet formation is affected bears a continuous relation to the temperature. There may be a minimum temperature, varying with the race, below which no further morphological change is elicited.

It has been the finding of all who have worked on *Daphnia* to date, with the exception of Woltereck and his students, that the nutrition of the mothers has little influence upon the relative helmet size of their neonata. In the earliest culture, experiments (Ostwald, 1904) done with the purpose of studying the causes of cyclomorphosis in *D. cucullata* (the species with which Woltereck worked), the mothers were very poorly fed. Yet at high temperatures their neonatae were born with high helmets. Wesenberg-Lund (1926) is of the opinion that nutrition cannot be the factor controlling cyclomorphosis. The regularity of the cycle (he says) is too great to allow its control by the highly variable level of natural nutrition. Coker & Addlestone were the first to show experimentally, using *D. galeata*, that females which gave every evidence of being well fed produced neonatae lacking spikes (= helmets?) if kept at a sufficiently cool temperature. Their transfer experiments showed (as Ostwald had indicated long before Woltereck) that the temperature which determines spike formation is that prevailing during the early and middle stages of embryonic development. Laboratory experimentation on a different race of *D. galeata* and *D. retrocurva* has indicated that the role of nutrition in controlling the embryonic phase of helmet formation is negligible. Of even greater importance is the present demonstration that nutrition in the lake plays no significant role in determining relative helmet size in the neonatae of the highly cyclomorphic *D. retrocurva*. There is every reason to believe that this is true for all species of the *pulex-longispina* group. This is complete refutation of Woltereck's assertion that temperature acts only upon the rate of the mother's nutritive processes.

As pointed out above, it had been the assumption of all workers prior to Coker & Addlestone that the same environmental factors controlled both the embryonic and the postembryonic phases of helmet development. There is now ample evidence that this is incorrect. Woltereck claimed on the basis of his experiments that the generation number as well as the nutritive level controlled post-embryonic helmet growth in *D. cucullata*. Berg (1936), experimenting upon the same population of *D. cucullata*, cast serious doubt on Woltereck's contention of the importance of generation number. However, this work did confirm Woltereck's claim that the helmets of *D. cucullata* in laboratory culture, under conditions of high temperature and good nutrition could grow

tachyauzetically. This is in sharp contrast to the findings of all investigators in the United States. In none of the American *Daphnia* is relative helmet growth in the laboratory tachyauzetie or even isauzetie. The species for which this has been demonstrated are spike-headed *Daphnia galeata* (Coker & Addlestone, 1938; Banta, 1939; present investigation), helmeted *D. longispina* (Banta, 1939) and *D. retrocurva* (Banta, 1939; present investigation). Unpublished evidence of the author indicates that the same condition obtains in two other races of helmeted *D. longispina*. No more can be said at this time than that the European *D. cucullata* appears to be different from the aforementioned American species with regard to the factors controlling post-embryonic helmet growth under laboratory culture conditions.

By means of relative growth analyses it is possible for the first time to measure the rate of relative helmet growth during post-natal life. In the lake the helmet of *D. retrocurva* grows isauzetically during the spring and early summer and tachyauzetically during midsummer. This change is not accompanied by any consistent trend in the nutritive level. The increased rate of relative growth occurs only when the temperature is above ca. 19° C. These higher temperatures seem to be a *conditio sine non* for tachyauxis. Although temperature might appear from study of the natural cycle as the sole factor controlling tachyauxis, the situation in laboratory culture indicates that its control is more complex. When *D. retrocurva* are cultured at temperatures above 19° C. under nutritive conditions which appear adequate in every other respect, the helmet grows less rapidly than the rest of the body. Even more strange is the fact that the rate of relative growth at 6°-7° C. is greater than it is at 21°-24° C.; at 10°-12° C. it is less than at either the higher or the lower temperature. This type of relationship between temperature and rate of relative growth suggests control by more than one factor. The action of at least one of these is variable with temperature. In the lake the rate of relative head growth is constant over a range of temperatures from 0° to ca. 19° C. Within this range animals in laboratory culture have several rates of relative growth. This suggests that the constancy of rate in the lake is due to control either by a smaller or a very much larger number of factors than are effective in the cultures. The former is considered the more likely. If that is the case, it is reasonable to suppose that the smaller number of factors acting in the lake are included in the complex acting in the laboratory cultures. The other elements of this complex, peculiar to the conditions of laboratory culture are as yet unknown. This "laboratory factor" acting with a positive temperature coefficient has a depressant effect upon the rate of relative head-growth.

Coker (1939) suggests that a "helmet inhibiting" factor is present in laboratory culture. The work with *D. retrocurva* has shown that there is not a complete inhibition of helmets as there is of the spikes on *D. galeata*. The phrase "helmet inhibit-

ing" has perhaps an incorrect connotation. He put forth two suggestions as to the possible nature of this laboratory factor; it might be a waste product of metabolism, or it might be due to the small size of the container. The difference in size between laboratory culture vessels and the pelagic region of a lake is enormous. It is possible that in some way the size of the *Lebensraum* might affect the metabolism of head growth. Gruber (1923) has indicated that the lengths of the mucrones and the head spike of *Scapholeberis mucronata* were relatively larger in lakes than in ponds. Experiments are planned which will attempt to investigate this possibility.

In Bantam lake post-embryonic growth of the helmets of *D. retrocurva* is isauxetic following varying amounts of embryonic helmet growth. Tachyauexis in the lake only occurs after the maximum neonate helmet size has been reached. The literature has been examined for information which would bear upon the generality of this relation. Wesenberg-Lund (1908) provides some from his observations on natural cycles. In both *D. cucullata* and *D. hyalina* (= *longispina*) the tallest helmets are produced by considerable embryonic growth followed by tachyauexis. The greater helmet size attained in *cucullata* is due to relatively larger neonate helmets in addition to a higher degree of tachyauexis. In all but one of the *cucullata* populations studied, as judged by his drawings, tachyauexis followed the attainment of the relative neonate helmet size maximum for that population. Due, however, to the length of the intervals between samples the significance of this conclusion is uncertain. The population in Sorösö is exceptional. Here tachyauexis clearly occurs before the attainment of maximum relative helmet in the neonatae. Wesenberg-Lund's sample of June 28 is of most importance. On this date for the first time that season young adults were found with helmets longer than the carapace,  $\frac{HL}{CL} = 1.05$ . The neonatae in the same sample have  $\frac{HL}{CL} = 0.85$ . Three weeks earlier the  $\frac{HL}{CL}$  ratio for neonatae was 0.80. The head length in the young adults mentioned therefore increased tachyauexetically. The maximum neonatae  $\frac{HL}{CL} = 1.0$  was attained by July 27, yet on that date the degree of tachyauexis appeared to be declining. The temperatures given are 15° C. for June 7, 17° C. three weeks later, and 16° C. on July 27. It is not possible on the basis of such mean data to draw any conclusions concerning the relation of temperature to the process of helmet growth. This is the only clear case of a disjunction of the two phases in the natural cycle.

In one instance experimental disjunction has been achieved in a population of *D. cucullata* in which tachyauexis in the lake normally follows the attainment of maximum neonate helmet size. The cycle in the lake (Frederiksborg Castle Lake) is outlined by Wesenberg-Lund (1926). Berg (1936) kept ephippia, which in the usual course of events would

hatch in early spring, in a refrigerator until mid-summer. The ephippia were then allowed to hatch (at an unspecified temperature). The roundheaded neonatae so produced were cultured at 22° C. with good nutrition. The head length increased tachyauexetically. The degree of tachyauexis was about the same in a laboratory culture vessel and in a gauze-ended container placed in the lake.

The available evidence for *D. retrocurva* and *cucullata* indicates that tachyauexis generally occurs in the lake only after the relative helmet length in neonatae has reached a maximum. However it would appear that the embryonic and post-embryonic phases can vary independently of each other. The relationship generally found in the lake may be due to the fact that each phase is dependent upon the temperature. There is, however, no direct evidence which contradicts the alternative view that in *D. retrocurva* the maximum relative helmet size of the neonatae is a necessary but not sufficient condition for tachyauexetic growth of the helmet.

### SUMMARY

1. The cyclomorphosis of a population of *D. retrocurva* in Bantam Lake has been followed from April to August by means of an analysis of relative head growth.
2. This has shown that the relative head length of the neonatae increased from April until the end of June. At this time a maximum was reached which was maintained until August 10, the end of series.
3. The relative neonate head length shows a close correlation with temperature.
4. From April until the middle of June the head grew at the same relative rate as the rest of the body. From then until Aug. 10, the head grew tachyauexetically. The degree of tachyauexis rose to a maximum value and then subsided, although it had not decreased to the level of isauxesis by Aug. 10.
5. Isauxetic helmet growth obtained over a range of temperatures from 8° to 19° C. Nutrition varied from good to very poor during the same period.
6. Tachyauexis in the lake only occurred at temperatures above 19° C. The degree of tachyauexis appeared to vary independently of both nutrition and temperature.
7. Culture experiments at various temperatures demonstrated that the relative head length of the neonatae is controlled primarily by temperature.
8. In laboratory cultures the relative growth of the head is bradyauexetic at all temperatures investigated. However, the rate of relative growth is not constant. It is highest at 6°-7° C., lowest at 10°-12° C.
9. This curious relation of rate of relative head growth in laboratory cultures to the temperature suggests that this may be due to the interaction of more than one factor. It is reasonable to suppose that one of these as yet unknown factors can be identified with that acting in the lake to produce isauxesis or, above 19° C., tachyauexis.
10. A population of *Daphnia galeata* was present in the Bantam Lake samples from the initial one in April until July 9. This *Daphnia* belongs to a race



similar to the one experimented upon by Coker & Addlestone. The cyclomorphosis in this population, consisting of the development of spike-heads, was subjected to a relative growth analysis.

11. The relative length of the neonate head is variable, but relative head length does not appear to be a satisfactory measure of the degree of change in head shape.

12. On the basis of head lengths, the relative growth of the head in the lake was bradyauxetic at all times. However, all individuals born in the lake with spike-heads retained the pointed condition throughout life.

13. The rate of relative head growth was constant from April 1 until the middle of May. After this date it was somewhat higher, reaching a maximum on June 14 and 28.

14. The events of this cycle follow in the same sequence as those for the *D. retrocurva* cycle. However, the increase of the relative rate of head growth over a previous constant level did not occur simultaneously in the two species.

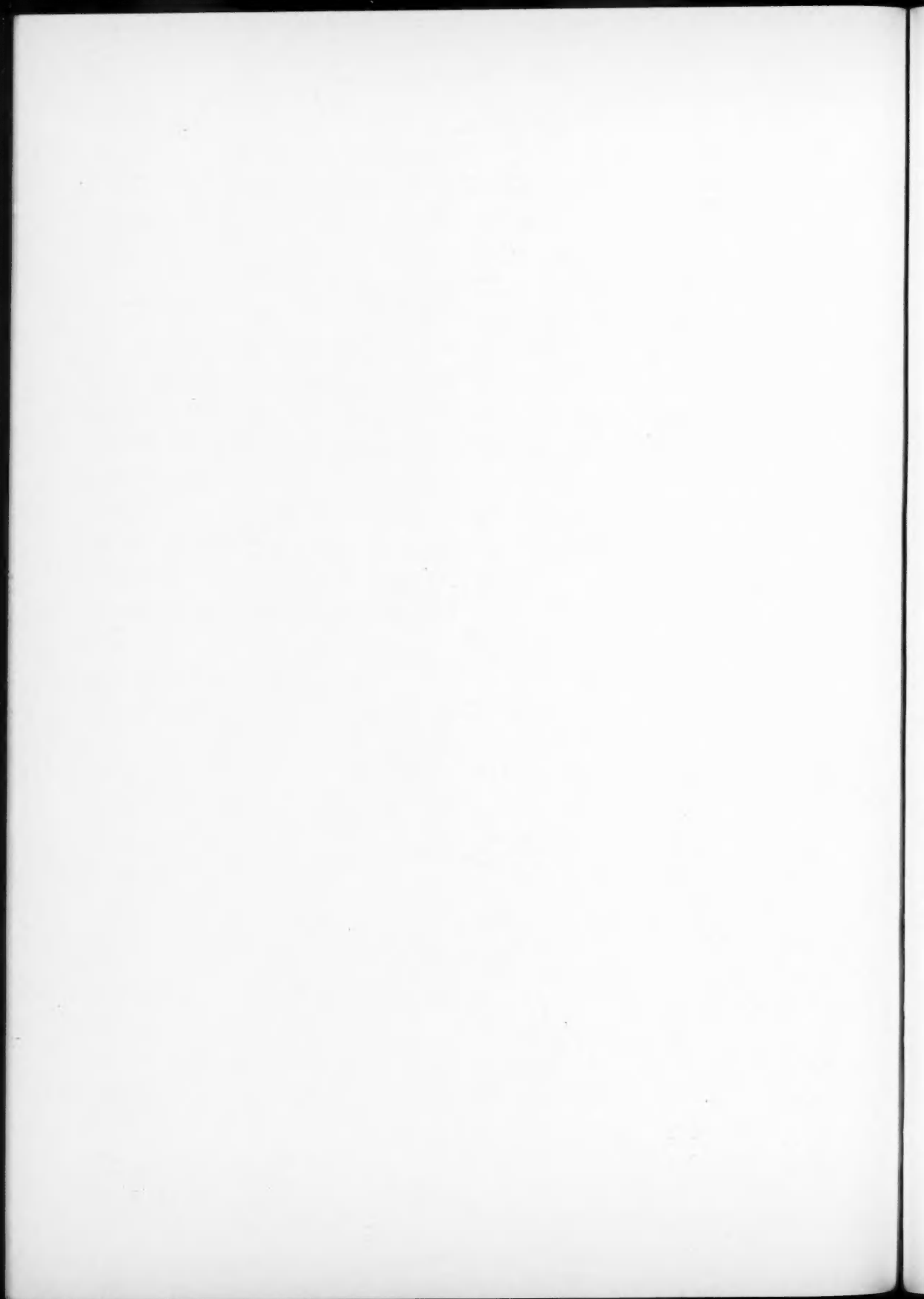
15. In laboratory culture it was possible to show that the neonatae which developed at temperatures below 7° C. are round-headed; those above 7° C. bear spikes. Hypolimnetic populations in lakes Highland and Shenipsit at 7°-8° C. had pointed heads. In the North Carolina race of *D. galeata* studied by Coker & Addlestone only roundheaded neonatae are born below 11° C.

16. Re-examination of the literature in the light of the results of the present investigation reveals two pertinent points. *D. cucullata* apparently resembles *D. retrocurva* in that the embryonic and post-embryonic phases can vary independently of each other. The helmets of *D. cucullata* can, however, grow tachy-auxetically in the laboratory with high temperature and good nutrition. This species thus differs from every other cyclomorphic species which has been studied up to the present time.

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REDUCTION OF UNGRAZED MIXED PRAIRIE TO SHORT  
GRASS AS A RESULT OF DROUGHT AND DUST

F. W. ALBERTSON

*Fort Hays Kansas State College*

AND

J. E. WEAVER

*University of Nebraska*

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# REDUCTION OF UNGRAZED MIXED PRAIRIE TO SHORT GRASS AS A RESULT OF DROUGHT AND DUST

## INTRODUCTION

Many marked changes have occurred over vast areas of native grassland in central North America as a result of the recent desiccation and wide-spread distribution of dust. The gradual replacement of true prairie by mixed prairie over an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota has been described (Weaver, 1943). Great changes in both true and mixed prairie as a result of long periods of drought have been recorded by Albertson and Weaver (1942) and Weaver and Albertson (1943, 1944). The present study of the gradual reduction of a typical area of mixed prairie to short grass without the impact of grazing has extended over a period of many years. It is illustrative of a very widely spread phenomenon that occurred mostly during the past decade.

Certain grassland areas lying south of Phillipsburg in north-central Kansas were selected by the second author in 1920 as typically representative of mixed-prairie vegetation. These were studied in regard to the plant cover and the environmental relations over a period of three years (Weaver, 1924). They have been re-examined almost every year since. The prairie lying 8 miles south of Phillipsburg is 130 rods long from north to south and 55 rods wide, and about 45 acres in area. It was one of the several permanent grassland stations maintained in mixed prairie by the authors during the many years of drought and the subsequent period of recovery.

## SOIL AND SOIL MOISTURE

The station is characteristic of the gently rolling topography of the general area. The fertile soil is a mellow, dark-brown, very fine sandy-loam of the Holdrege series. At a depth of 12 to 15 inches it is slightly lighter in color and contains enough clay to be quite sticky, although when wet it is dark in color to a depth of 2 feet. Below this level it is light yellow and shows throughout its loess origin. It is not acid at any depth. The mellow subsoil is very deep. The hygroscopic coefficients are about 11 percent in the first foot, 12.5 in the second and third, and 10 to 11 percent to 5 feet in depth. The organic matter in the soil averaged 4.56 percent and the nitrogen 0.206 percent. A mechanical analysis is given in Table 1.

The mean annual precipitation is 23.2 inches but in certain years following heavy rainfall the soil has been well moistened to a depth of 8 feet. In other years the deeper subsoil had no water available for plant growth and drought in the upper

TABLE 1. Mechanical analyses of soils from Phillipsburg, Kansas.

Depth, feet	Coarse gravel	Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
0.0-0.5....	0.0	0.0	0.3	0.2	1.2	43.5	35.8	19.0
0.5-1.0....	0.0	0.0	0.0	0.2	0.5	44.4	32.8	22.1
1-2 ....	0.0	0.0	0.0	0.2	0.3	39.7	34.0	25.8
2-3 ....	0.0	0.0	0.0	0.3	0.6	41.2	31.9	26.0
3-4 ....	0.0	0.0	0.0	0.1	0.2	37.5	31.4	30.8

soil was of common occurrence. During three years of approximately normal precipitation (1920 to 1922 inclusive) soil moisture was ascertained (Clements and Weaver, 1924). In 1920, July and early August were periods of soil drought and, at times, of actual deficiency of available water. During 1921, water available for growth was almost exhausted one week in July and two in August; no water was available to a depth of 4 feet late in August. The next year, a period when little or no water was available in the soil occurred in June, and this condition was nearly constant from the middle of July until late in autumn. Hence, the plants of this prairie are often subjected to moderate drought even during years of normal precipitation.

## VEGETATION

The vegetation was typical mixed prairie, the mid grasses alternating with or forming a layer above the shorter ones. Little bluestem (*Andropogon scoparius*), side-oats grama (*Bouteloua curtipendula*) and western wheat grass (*Agropyron smithii*) were the chief mid grasses. But tall grasses occurred abundantly on the moist slopes, in ravines, and on level land where there was little runoff. Most abundant among these were big bluestem (*Andropogon furcatus*), Indian grass (*Sorghastrum nutans*), and nodding wild rye (*Elymus canadensis*). The short grasses consisted chiefly of blue grama (*Bouteloua gracilis*) with buffalo grass (*Buchloe dactyloides*) usually more or less intermixed. They occurred on the drier slopes in pure stands but were found more or less throughout, except under dense patches of big bluestem and other taller grasses where light was greatly reduced. The forbs were those typical of mixed prairie; the absence of certain less xeric species common eastward and the presence in abundance of more westerly species indicated a drier climate than that of true prairie. Among the latter were *Astragalus mollissimus*, *Oxytropis lambertii*, *Malvastrum coccineum*, *Opuntia fragilis*, and *Sideranthus spinulosus*. Further description here seems

unnecessary, since the behavior of the various components of the vegetation will be discussed. In this prairie, half-square meter samples of soil containing the underground parts of pure stands of big bluestem, western wheat grass, blue grama, and buffalo grass were obtained by Shively and Weaver in 1936 in their study of the amount of underground plant materials in different grassland climates (1939).

#### EARLY RESULTS OF DROUGHT

A careful survey late in June, 1934, after a single year of drought and dusting revealed that much damage had been done. The basal cover was far less than normal. There were many places where the grass had been covered with 0.5 to 2.5 inches of dust. This had been compacted by rains and the grasses were dead or dying. The deeper the dust burial the thinner was the stand of big bluestem. There were great losses of blue grama and especially of buffalo grass in the alternates of short grass. There were many clumps of half-dead sand dropseed (*Sporobolus cryptandrus*). No living little bluestem, needle grass (*Stipa comata*), June grass (*Koeleria cristata*), or low-growing panic grasses were found. *Antennaria campestris*, *Viola papilionacea*, *Astragalus crassicaerpus* and various other forbs of the understory were likewise killed.

The whole prairie had been covered with dust. Over half of it the dust was at least 0.25 inch deep and much vegetation over several acres of the north end had been covered to a depth of 0.5 to 2.5 inches or even more. Here, especially, great losses had occurred. In the deeply dusted<sup>1</sup> part all native grasses had been killed or at least only a few bunches per square meter remained (Fig. 1). Frequently the lowest joints of *Opuntia humifusa* were entirely buried and only a few green tips of big bluestem were seen. While the following weeds were scattered in patches or as individuals throughout the whole prairie, here they occurred in great abundance. The chief species were lamb's quarters (*Chenopodium album* and *C. leptophyllum*), peppergrass (*Lepidium densiflorum*), Russian thistle (*Salsola pestifer*), fox-tail (*Setaria viridis*), sunflower (*Helianthus annuus*), pigweeds (several species of *Amaranthus*), and cocklebur (*Xanthium commune*). The general level of pigweeds was about 9 inches, but sometimes patches twice this height occurred. Thus, the whole prairie had a peculiarly irregular or ragged appearance; over half its area it could not be distinguished from a very weedy pasture.

Deeply dusted and extremely weedy places also occurred at the south end where big bluestem had lost more than half of its territory by dusting and drought. A new growth of some deeply buried big bluestem had reached a height of 2 to 3 inches but the plants were dying from lack of water, since the compacted dust furnished an efficient barrier to penetration of rain. While many dead bunches of vari-



FIG. 1. Typical view in drought-stricken and dust-covered portion of prairie. Only a few relict bunches or patches of short grass remain. Russian thistle (*Salsola pestifer*) and witchgrass (*Panicum capillare*) are beginning the subere.

ous grasses occurred, the best evidence of destruction was the open cover and much bared ground. The death of little bluestem seemed to be total, but loss of big bluestem was about 35 percent.

In this scene of destruction spring rains had resulted in an excellent growth of much remaining big bluestem over considerable areas. Blue grama and buffalo grass were flowering abundantly. In the opened cover the stolons of buffalo grass were the best developed in many years. These grasses were thriving even where partially buried by dust. Many of the taller and deeply rooted forbs remained. Chief among these were *Kuhnia glutinosa*, *Solidago glaberrima*, and *Psoralea tenuiflora*. But even these had been greatly reduced in numbers. *Malvastrum coccineum* was not affected; *Gaura coccinea* was common. *Ambrosia psilostachya* had greatly thickened its stands in ravines; *Aster multiflorus* and *Solidago mollis* had become a brush-like growth where vegetation on lower slopes had been greatly thinned or disappeared. Other species present included *Sideranthus spinulosus*, *Opuntia humifusa*, *Lygodesmia juncea*, *Allionia linearis*, *Allium nuttallii*, and *Anemone caroliniana*. These have been pointed out previously by the writers as being among the most drought resistant forbs of mixed prairie (Weaver and Albertson, 1940).

#### ALTERNATING MOIST PERIODS AND DROUGHT (1935-1939)

This five-year interval will long be remembered as one of intense drought alternating with periods of rainfall sufficient to revive the vegetation and even promote vigorous growth. But decreases or loss of certain species always equaled or exceeded the gains made by others. The net result was a gradual decrease in tall and most mid grasses and less xeric forbs, offset by an increase in short grasses and side-oats grama. A transient population of annual

<sup>1</sup> Dusted is a colloquial term meaning covered with dust



weeds, although often greatly dwarfed, was characteristic.

By June of 1937 the short grass portion of the cover had been reduced to about 25 percent of its former abundance. This reduction was not uniform but ranged from no loss in some favored places to 80 percent destruction in others (Fig. 2). Death of big bluestem also averaged about 25 percent but varied from 0 to 50 percent. Only dead bunches and no living shoots of little bluestem were found. Over the deeply dusted portions 80 percent or more of the cover of grasses had disappeared.



FIG. 2. Blue grama (*Bouteloua gracilis*) making an excellent growth during a favorable season in the drought years. Note that more than half of the soil surface is bare.

The short grasses were thriving due to early summer rains and lack of the competing mid-grass layer. The tufts and patches of buffalo grass, which were less abundant than those of blue grama, were enlarging rapidly by the spreading of long runners over the dead crowns of the taller grasses. Blue grama increased its hold by filling its crown area with stems and by extending the periphery by means of new tillers. New tufts were established from seedlings. The foliage cover of these survivors spread far more widely than normally. In patches of buffalo grass the foliage cover was usually 80 to 100 percent, due in part to an enormous production of stolons. Many bare interspaces were occupied by annuals such as species of *Chamaesyce*, *Panicum capillare*, and *Eragrostis cilianensis*.

By the autumn of 1937 the short grasses ranked first in abundance with blue grama forming by far the most of this type of vegetation (Fig. 3). Side-oats grama, a species which increased greatly during certain years with moist springs, held second rank (Fig. 4). Big bluestem was reduced to third place. Blue grama and side-oats grama had produced a good seed crop but buffalo grass and big bluestem failed in this important function.

Examination in late May, 1939, revealed that side-oats grama had increased enormously. Many of



FIG. 3. Photo Aug. 26, 1937, showing replacement of bluestem grasses (*Andropogon furcatus* and *A. scoparius*) over a north-east slope in the Phillipsburg prairie. The prairie in the background had long since been reduced by grazing to a buffalo grass disclimax.

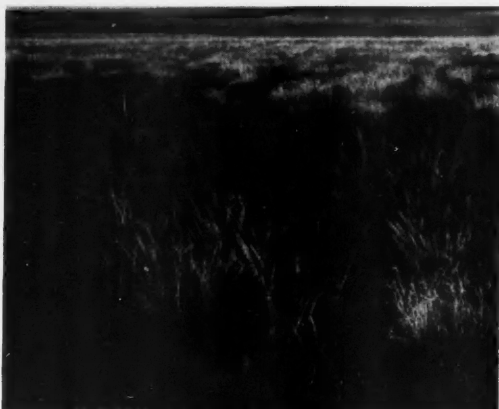


FIG. 4. Beginning of the side-oats grama (*Bouteloua curtipendula*) type (foreground) in soil almost bared by several years of drought. Aug. 26, 1937.

the bunches were 8 to 14 inches in basal diameter. This grass ranked as the most important dominant (Fig. 5). In other areas bunches of relict blue grama were pronounced. It also had increased very greatly and ranked second in importance. When peppergrass and plantain (*Plantago purshii* and *P. spinulosa*) were removed the wide spacing of the bunches was clearly revealed. The prairie had not been mowed the preceding autumn, which was the usual practice, and the old forage crop remained. The spreading of buffalo grass during the drought period of 5 or 6 years now gave it third place in abundance. So great was the desiccation that only small amounts of big bluestem survived in areas where it had been abundant. Some of the space had been occupied by sand dropseed, which was the fourth grass in importance. Most of the bare

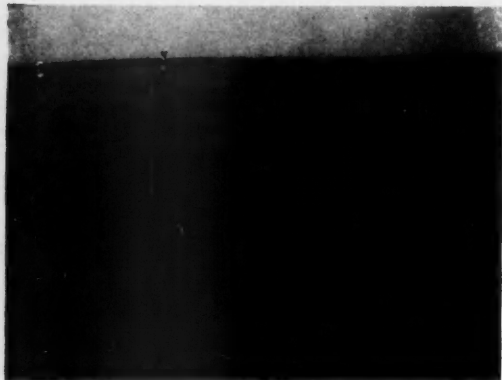


FIG. 5. Dense, almost continuous stand of side-oats grama on level upland in the Phillipsburg prairie. May 25, 1939. The flower stalks are those of the preceding year.

ground everywhere was covered with weeds. Tall dropseed (*Sporobolus asper*) and nodding wild rye occurred, the first rather abundantly in patches (Fig. 6).

A second examination late in August confirmed these conditions. The widely spaced bunches of side-oats grama composed an open basal cover of about 10 percent; the foliage cover was very much greater. There was as yet no understory of short grasses. These occurred in scattered patches of various sizes, but often of only a few square feet. Such patches very abundant, and islands of buffalo grass about ten square feet in area were very common. Stolons of this grass had often grown directly through bunches of blue grama and sand dropseed. Since there was no mowing, the mat of stems and leaves of buffalo grass, 4 to 6 inches thick, was piled about the bases of the mid grasses and stolons extended through the bunches. Because of the reduced water supply, even the greatly thinned stands of big bluestem could barely survive.



FIG. 6. Increase of tall dropseed (*Sporobolus asper*) after the cover of climax grasses was broken by drought. May 25, 1939.

In the small to large open spaces, abundant everywhere, seedlings of buffalo grass of the previous year had developed into many new tufts. This was also true of blue grama and side-oats grama. There was considerable tumblegrass (*Schedonnardus paniculatus*). Only a few bunches of wiregrass (*Aristida purpurea*) remained alive. All of the forbs previously mentioned as relicts still remained.

Most of the bared soil was occupied by annuals. These were thickest where there was some degree of shading, that is in the smaller bared places. But many irregular, large bare areas 6 to 10 inches in length were also more or less completely occupied by weeds. By far the most abundant were little barley (*Hordeum pusillum*) and peppergrass, but stickseed (*Lappula occidentalis*) was plentiful. The rough pennyroyal (*Hedeoma hispida*) was common, and plantain was abundant in the short grasses. Size of these annuals varied from season to season. During the driest years, as 1939, they seldom exceeded 2 to 3 inches in height and those of later germination barely protruded through the soil surface when overtaken by drought. They often dried prematurely and produced little or no seed since not infrequently they were sustained only by soil moisture supplied by melting snow.

#### PERIOD OF MOST CRITICAL DROUGHT

Following the cumulative effects of dry years, the autumn and winter of 1939-40 were extremely dry, and the year 1940 was one of severe drought. The prairie had been mowed about 3 inches high the preceding autumn. In May, examination of typical areas where side-oats grama dominated showed that the basal cover was not more than 8 to 10 percent, and sometimes much less (Fig. 7). The bare soil between the bunches was covered with hosts of annual weeds, since there was enough soil moisture in early spring to permit seed germination. The weeds were spaced so closely that not more than 10 percent of the soil was bare. They were chiefly stickseed and peppergrass but wild mustard (*Sophia multifida*) and

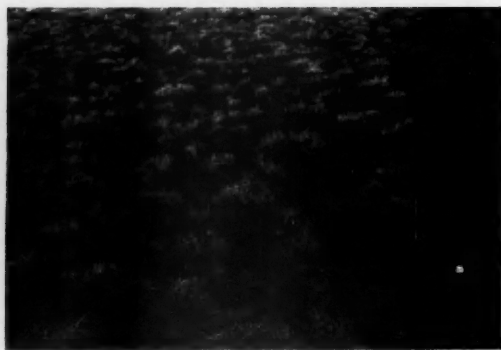


FIG. 7. Photo in stand of side-oats grama mowed the preceding fall. White patches are the bases of the bunches; the soil between them was clothed with a host of annual weeds. May 25, 1940.

plantain were abundant locally. In areas where snow had accumulated and in melting moistened the soil, little barley grew thickly. Russian thistle and pigweeds also occurred abundantly in places, and common sunflower in the most disturbed parts. The sod of blue grama, originally a cover of 80 to 95 percent, was broken up into a pattern of isolated bunches with a basal area rarely exceeding 20 percent.

#### BEGINNING OF DOMINANCE OF SHORT GRASSES

Conditions at an examination early in June, 1940, were almost tragic. Drought the preceding autumn was so drastic that only a little vegetation was left alive for spring growth. There was a dense cover of low, weedy plants such as peppergrass, stickseed, and plantain. But the relict short grasses had made only a little growth and were becoming dormant. Side-oats grama was practically all dead but there were scattered shoots of sand dropseed growing in a few of the widely spaced crowns. The occurrence of tufts and small bunches of blue grama almost everywhere showed clearly the great spread of this species, just as its thickening in places formerly occupied showed its ability to grow during drought when most other grasses succumbed (cf. Weaver and Darland, 1944). The most spectacular fact, however, was the wide spreading of buffalo grass. From wind-blown and animal-carried seed supplied by earlier, well established plants and from adjacent pastures, it had developed countless new bunches or small tufts. Indeed, it seemed almost as abundant and as widely distributed as blue grama. On the drier slopes where it had previously occurred in this mixed prairie, it had spread widely taking over the soil left bare by the dead mid grasses. This had also taken place over considerable portions of the adjacent, dusted, level areas. Here the replacement of mixed prairie by a short grass disclimax was well advanced. Elsewhere the process was under way. It seemed that short grasses might dominate the whole prairie.

By the middle of June the drought was so severe that blue grama was becoming dormant. The new growth of leaves had rolled when only 3 to 5 inches long and many had lost their green color. Many large bunches had dead centers with only a peripheral fringe of new growth. Leaves of buffalo grass had twisted spirally and were only half green. The new stolons were also drying. Side-oats grama was practically all dead and had made no new growth. Bunches of sand dropseed were still alive, but new shoots were few and the leaves were rolled tightly. The few scattered bunches of wiregrass were in a similar condition. Western wheat grass, which grew only in old haystack bottoms, along fences, and on protected but deeply dusted slopes, was much wilted. Even the annual weeds were very much dwarfed and wilted, except in places where snow had accumulated and in melting supplied extra soil moisture.

Late in August of 1940, this grassland no longer

had the appearance of a mixed prairie, but that of a depleted short grass disclimax. This change in appearance was due to the loss of nearly all of the taller grasses and the wide distribution of short grasses. Side-oats grama, so abundant the preceding year, had suffered an almost total loss. The dead bases occurred almost throughout. Only in a few places were bunches found that still showed life in the crown. Nodding wild rye and Indian grass, found locally and sparingly the preceding year, had succumbed. Western wheat grass was entirely dried; the invading sand dropseed, which formerly grew in a few patches, was dead. Nor was any trace of living little bluestem or big bluestem to be seen. In fact, the short grasses alone had made a fair growth and although developing slowly they were reclothing the soil (Fig. 8).



FIG. 8. General view on August 25, 1940, showing dead bunches of side-oats grama and spreading of blue grama and buffalo grass (detail in foreground). Much of the bare soil is obscured by dried annual weeds.

The drab or gray color in August was due largely to the dense population of dried stickseed and the lighter gray to dried plants of little barley intermixed with those of peppergrass. All of these weeds were only 4 to 8 inches tall, little barley having dried when the spikes were only half exerted from the protecting leaf sheath. Even the taller weeds as Russian thistle and lamb's quarters were only about a foot in height, so severe was the drought. This dull background was lightened by the bright straw-colored and dormant buffalo grass. The cover of native plants, which consisted almost entirely of the two short grasses, did not occupy more than 5 to 6 percent of the soil. Patches of bare ground occurred everywhere, varying from a few square inches to a few square yards in area.

Native forbs had been greatly decimated both in species and numbers. *Solidago mollis* was the only one that was fairly widely distributed; it formed conspicuous societies in some ravines. Its xerophytism was shown by profuse blossoming in this graveyard of dead plants.

A complete list of the perennial plants observed included only 11 species. These were *Malvastrum coccineum*, *Opuntia humifusa*, *Lygodesmia juncea*,

*Kuhnia glutinosa*, *Sideranthus spinulosus*, *Gaura coccinea*, *Allionia linearis*, *Anemone caroliniana*, *Solidago mollis*, the very deeply rooted *Psoralea tenuiflora*, and *Vernonia baldwini*, the last being confined to ravines. All were much dwarfed; nearly all including cactus showed wilting; many had not blossomed.

#### SPREADING OF SHORT GRASSES (1941)

Heavy rainfall followed the dry years just described. In April precipitation totaled 5.6 inches. That of May was 2.5, but June had a total precipitation of 8.7 inches. Thus, the soil which lacked available water for plant growth almost continuously in 1940 was now wet or at least moist to 5 feet in depth (Fig. 9).

Environmental conditions were conducive to growth but, except for the short grasses which had steadily increased during the preceding years of drought, there was little vegetation left to profit from the changed environment. In many places no perennial grasses could be found even in June. This was especially true in areas previously occupied by side-oats grama and sand dropseed. Nearly all of the bunches of these grasses failed to revive; in others it was not uncommon to find only a few living tillers protruding from the edges of the clumps. But where short grasses had grown, most of them had survived. They were handicapped, however, by the excellent growth of little barley 12 to 20 inches tall

which occurred in thick stands locally. After ripening it had lodged at a height of 3 to 6 inches, thus producing dense shade. Even in the best stands of buffalo grass this annual grew plentifully and the short grass was much shaded. In thin stands of buffalo grass it was so abundant that it was very harmful in reducing the light in addition to absorbing large amounts of water. The seed had germinated in fall and the plants grew rapidly early in spring, overtopping all of the other vegetation. The growth of the short grasses was greatly suppressed. The tillers of blue grama were much attenuated and light green in color as was also the foliage on the stolons of buffalo grass. The yield of the little barley alone averaged a ton per acre.

Seedlings of perennial grasses were rare. Nearly all had germinated following showers during the dry years. Here, as elsewhere over the broad expanse of the mixed prairie, a good year for the production of seed followed by another year favorable for the establishment of seedlings was required for revegetation by native grasses, except buffalo grass (Weaver and Mueller, 1942). But the annuals, little barley, peppergrass, and stickseed were scattered, unusually thickly, over the otherwise bare soil.

By midsummer the stolons of buffalo grass had spread widely and the foliage was unusually well developed. Blue grama and small amounts of surviving side-oats grama and sand dropseed had produced flower stalks. Many open places bare of native

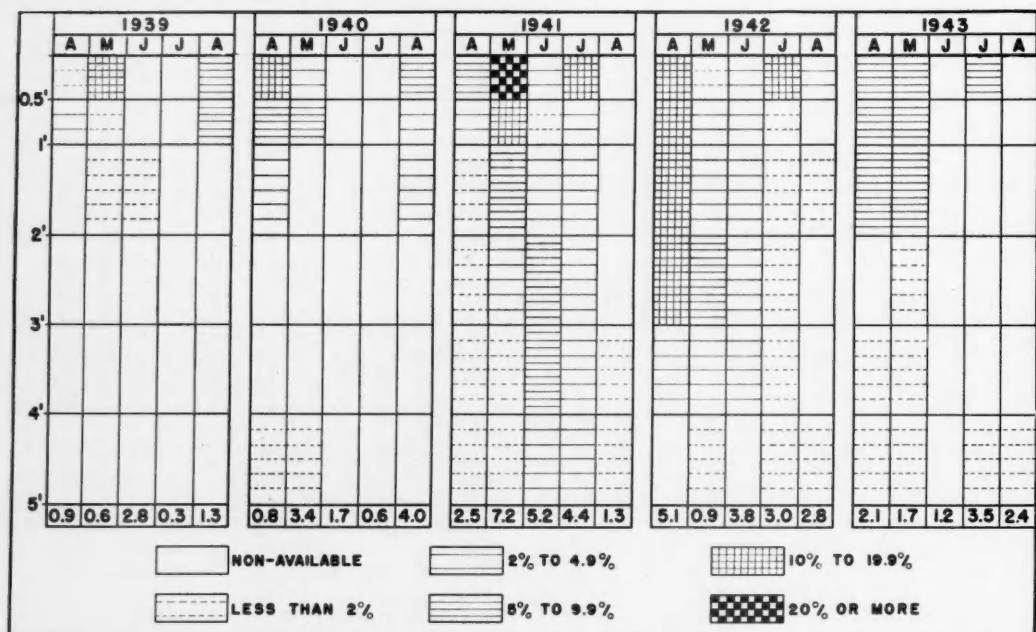


FIG. 9. Available soil moisture to a depth of 5 feet each month of the growing season in the prairie at Phillipsburg, Kansas, in 1939 to 1943, inclusive. Letters at the head of the columns indicate the months, and numbers at the foot show the current monthly rainfall. Data for 1944 (not shown here) are very similar to those in 1943.



vegetation were clothed with witchgrass (*Panicum capillare*), Russian thistles, and pigweeds. The witchgrass was of great size, often plants were 3 feet in height and width. It formed dense, large patches. Growth continued into September. For the first time in many years a few flower stalks had been produced by relict big bluestem. The short grasses had consolidated their gains and almost completely covered many areas locally.

In some ravines western wheat grass had replaced all other native grasses, but this condition was local. It also had complete occupation of other small areas where drifts of dust had been deposited by the wind. It grew in pure stands and was spreading from areas disturbed by stacking hay.

After prolonged study, it was estimated that the soil over 30 percent of the entire prairie was without a long-lived cover. Of the remainder, about 78 percent was occupied, usually by open stands of short grass, but over a third of this, short grasses were dense enough to make the invasion of mid grasses difficult. Side-oats grama, widely scattered and in a drought-weakened condition occupied 12 percent, tall dropseed about 8, and western wheat grass the remaining 2 percent.

The prairie had the aspect of a short grass climax except for the open alternates of side-oats grama and bared places with widely scattered bunches of tall dropseed. Perennial forbs were not conspicuous. But the tall plants of common sunflower, lamb's quarters, and other weeds indicated the open cover or bared soil elsewhere.

The following lists of grasses or grass-like plants, forbs, and ruderals constituted the vegetation. The grasses are arranged in order of their abundance, the last three being rare.

Buffalo grass  
Blue grama  
Side-oats grama  
Tall dropseed  
Sand dropseed  
Western wheat grass  
Nodding wild rye  
Tall panic grass  
Big bluestem  
Wiregrasses  
(*Spp. of Aristida*)  
Six-weeks fescue  
(*Festuca octoflora*)  
Scribner's panic grass  
(*Panicum scribnerianum*)  
Carex  
(*Carex praegracilis*)

All of the forbs previously listed for 1940 persisted but they were greatly reduced in number. They were all that remained of a predrought list of more than 50 species. Annual weeds composed a long list as follows:

*Amaranthus graecizans*  
*Amaranthus retrofractus*  
*Bromus tectorum*  
*Chamaesyce* spp.

*Chenopodium album*  
*Eragrostis cilianensis*  
*Helianthus annuus*  
*Hordeum pusillum*  
*Lappula occidentalis*  
*Lepidium densiflorum*  
*Leptilon canadense*  
*Mollugo verticillata*  
*Panicum capillare*  
*Plantago purshii*  
*Plantago spinulosa*  
*Polygonum ramosissimum*  
*Salsola pestifer*  
*Sophia multifida*

#### CONTINUED SPREADING OF SHORT GRASSES AND CONSOLIDATION OF THE COVER

Late in August, 1942, the prairie was green and in a thriving condition. One could scarcely recognize it as the old prairie with the broken-down cover (Fig. 10). The short-grass type presented a wonderful appearance with an average basal cover of 50 percent and a foliage cover varying between 80 and 100 percent. About 60 percent was blue grama and nearly all of the remainder buffalo grass. The old alternates and scattered patches of short grass had merged over many acres to form a continuous expanse of this type. Blue grama had an abundance of flower stalks which portended a good crop of seed. Buffalo grass had already produced seed but relied mostly on vegetative propagation. The carpet of short grasses was 6 to 8 inches thick. Throughout the entire prairie, large pure alternates of short grass were found. The trend nearly everywhere was toward short grasses. Closing of the mat had excluded nearly all of the weeds both annual and perennial.



FIG. 10. View in the prairie on August 21, 1942. Note the thriving bunches of side-oats grama and the carpet of short grasses with blue grama in blossom.

A second, smaller type was dominated by side-oats grama. It was being invaded along many lines of contact by buffalo grass and blue grama. This type occurred as alternates, both large and small, in the widely spread short-grass cover. The mid-grass



cover formed by side-oats grama was often quite open. The bunches were rather regularly widely spaced but of large size. Often witchgrass formed conspicuous stands between them; the purplish panicles, which were densely aggregated, reached a height of 1.5 to 2 feet. In only a small portion did the foliage cover of side-oats grama alone completely conceal the soil; nearly always there was abundant room for invasion.

A small part of the prairie, probably only 4 to 5 percent, was still dominated by weeds, and a few small spots by grasses other than the three great dominants. Small amounts of tall dropseed were found; often the plants were widely spaced. Certain older stands had been nearly replaced by the invasion of buffalo grass. Sand dropseed formed a few, dense, nearly pure stands in dust-covered soil and some was scattered thinly in the side-oats grama, but its importance was not great. One ravine was mostly filled with a pure stand of western wheat grass, the former cover of tall panic grass having been reduced to a narrow patch only 15 feet long. Up the ravine, above the wheat grass, the largest area of big bluestem was found. It was about 10 feet wide and 45 feet long, tapering thereafter into a very narrow belt down to the wheat grass. Elsewhere, it occurred only rarely and as isolated bunches usually a square foot or less in area. But it had flower stalks 4 to 6 feet tall, and seedling bluestems were found about the parent plants. It was a pitiful "last stand" of this grass which was at one time one of the most abundant dominants. In other former strongholds it had completely failed. Little bluestem fared even worse. It was found very sparingly in one limited area on a north slope. Only a trace of wiregrass was seen. Except for a trace of nodding wild rye, tall panic grass, and a very little big bluestem, the whole deeply dusted northern portion of the prairie had now been occupied by western wheat grass.

A deep gray mulch of the dried and lodged stems of little barley was very common. *Panicum scribnerianum* and *Eragrostis spectabilis* showed their return in some places. The wider the spacing of the perennial grasses, the more weeds found room for growth. In places tumblegrass occurred, and prostrate spurge spread widely over the thick mulch at a height of 3 to 4 inches. Despite the carpet of little barley, seedlings of blue grama and tumblegrass were found commonly, and those of side-oats grama were plentiful. In fact, plants in all stages of development were observed as a result of growth during the wetter years. In some recently severely dusted areas, weeds were few and the seedling crop of grass, especially side-oats grama, was much larger. Buffalo grass showed vigorous but recent invasion in the periphery of many stands of this grass. Here too, seedlings of blue grama were common.

Transitions between small weedy areas and those with short grass or side-oats grama were common but not extensive. Here, as in the weedy patches, the perennial grasses had suffered the greatest losses

by drought or dust burial. The relict old bunches of blue grama were noticeably large; some measured 12 to 18 inches in basal diameter and the top spread was fully 3 feet.

*Ambrosia psilostachya*, whose rhizomes endured the drought, was the best indicator of bare soil or soil with only a few relict bunches of blue grama or buffalo grass. It occurred in streaks or small patches. Although large isolated plants of *Helianthus annuus* and *Gaura parviflora* occurred, the prairie was not weedy and in general it was far beyond the ruderal stage. Because of the excellent year for growth, all species flourished.

As to forbs, they were few to rare. There were no societies, except of *Solidago mollis* in one ravine. Even it had previously lost greatly in both numbers and stature.

In July, 1943, the accumulated debris under the short grasses was rather regularly 4 to 5 inches deep and sometimes 8 inches (Fig. 11). The new foliage of buffalo grass was 9 inches tall and that of blue grama 12 inches. Stolons of buffalo grass often extended over this carpet 7 or 8 inches above the surface of the soil. Growth of these grasses was dense and the foliage cover usually 100 percent. The preceding year's flower stalks of blue grama were sometimes 22 inches tall, so favorable had been the water relations. The former bare spaces in the short grass cover were now filled by young plants of blue grama or by the runners of buffalo grass which sometimes spread 11 inches from the base of the tufts.



FIG. 11. View in short grass type on July 7, 1943. Note large isolated bunches of blue grama which are closely surrounded by mats of buffalo grass.

Little barley was almost absent from the short grass. Many large bunches of both blue grama and side-oats grama had died, apparently smothered by the debris. But this excellent forage did not cover the whole prairie. Where there were still interspaces, many remarkably well developed annuals occupied the soil (Figs. 12 and 13).

Large bunches of side-oats grama were scattered more or less throughout. Those in the short grass were beginning to be invaded by buffalo grass but elsewhere this grass in many places formed practically pure stands several rods wide. To a limited



FIG. 12. Horseweed (*Leptilon canadense*) growing in small bare spaces where the mat of short grasses is still open (Aug. 27, 1943).



FIG. 13. Excellent development of pure short grass in foreground and weeds, mostly horseweed, in background. July 7, 1943.

extent, western wheat grass had spread to form an upper layer over the short grasses. Large, isolated, circular patches of buffalo grass alternated in the most disturbed places with wheat grass or with ruderals, mostly horseweed. Because of the occurrence of many bare places and the unusually rank growth of various annual weeds, as common sunflower and horseweed, in them, the whole prairie had a weedy aspect. The fewer the weeds the denser was the cover of grasses. Certain grasses, such as nodding wild rye, purple lovegrass (*Eragrostis spectabilis*), and wiregrass were found, as well as considerable sand dropseed in the bare places. There were only a few scattered bunches of big bluestem. Forbs were few but the number of species had increased.

By August of 1944, the short grasses had extended their area greatly and in most places consolidated it into an almost continuous cover. Of this buffalo grass formed by far the larger part. Any relict sand dropseed was closely invaded and the bunches often reduced to 1 or 2 stems. Even bunches 8 inches in diameter were threaded through with stolons. Bunches of side-oats grama were suffering a similar fate. Only the centers of large and numerous patches of this grama scattered in the short grass area were

free from the invading buffalo grass. This grass had now closed in completely around the bunches of blue grama and was beginning to reduce its height growth and to prevent vigorous peripheral tillering. Although there were still many patches of sunflower and witchgrass, buffalo grass was not greatly retarded in its invasion.

Some relict grasses, though few in numbers, as big and little bluestem and tall panic grass, were thriving in the most mesic places. *Solidago mollis* and *Ambrosia psilostachya* were very vigorous and locally abundant. Western wheat grass continued to spread rapidly, and relict bunches of big bluestem on the level upland, where it had been dormant for several years, put forth flower stalks. Side-oats grama was by far the most abundant of the taller grasses.

Viewed as a whole, bluestems and other predrought mixed-prairie grasses had probably reached their lowest ebb. Several tall and mid grasses in ravines had been almost replaced by western wheat grass. The abundance of sunflowers and witchgrass was somewhat misleading. The tall growth of the composite tended to overemphasize the amount of bare

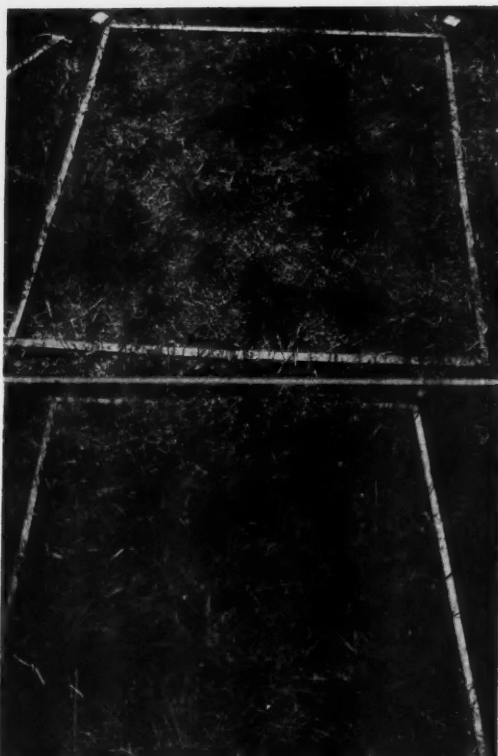


FIG. 14. Quadrat 1 of blue grama and buffalo grass, (upper) in autumn of 1940, when the basal cover was about 15 percent. (Lower) View in September, 1942, when the basal cover had increased to 61 percent. Two years later it was 95 percent.

area; witchgrass obscured many of the scattered bunches of other grasses. The short grasses had replaced most coarse annual weeds and over much of the prairie the short grass mats were continuous. But side-oats grama was also widely spread and held the rank of the most abundant taller grass.

#### THE RECORD FROM QUADRATS

After thousands of years of adjustment and readjustment of the species of this mixed prairie to the vicissitudes of climate and the bright prospects for a new cover of short grasses, it had abruptly reached the end of its life-span. In 1945 the land was broken by plowing. A brief record of its last 5 years, however, was obtained by a series of permanent meter quadrats which were installed in 1940. These had been placed at random along four lines extending parallel throughout its width. They were first charted with a pantograph in the fall of 1940 when the population of perennial plants was at low ebb. Eleven of the quadrats occurred in places where short grasses were dominant (Table 2). The slow but steady gain of blue grama from 8.8 to 25.2 percent during 4 years was surpassed by the spread of buffalo grass. From a cover of 4 percent in 1940 it increased to 45.5 by 1944. A few other perennial

grasses occurred in small amounts; native forbs and weeds were not charted (Fig. 14).

In quadrats dominated by blue grama, in the absence of buffalo grass, the increase was only from 8.8 to 15.1 percent (Table 2). This was about doubling the original basal cover in the period in which buffalo grass increased 11 fold (Fig. 15). In five quadrats where the original area of side-oats grama was 1.7 percent, the basal cover of this species increased gradually to 31.5 percent (Fig. 16). That of sand dropseed decreased. In other quadrats where the four chief grasses were intermixed, buffalo grass increased most rapidly, from 1.2 to 34.6 percent, side-oats grama was second (0.8 to 13.5 percent), but blue grama and sand dropseed did more poorly (Table 2 and Fig. 17).

The total basal cover of perennial grasses in each quadrat of the several groups is shown in Table 3. In the blue grama-buffalo grass cover there was a good increase in each quadrat every year. The actual basal area by years was 13, 36, 48, 61, and 72 percent. Increase in the quadrats of blue grama was not so great nor so uniform. Gain in basal cover of side-oats grama was not always uniform year by year, but the average basal area increased steadily

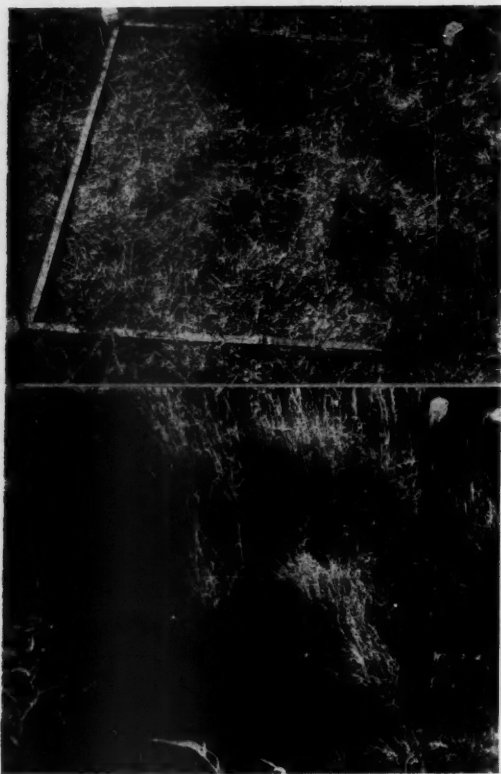


FIG. 15. Quadrat 14: (upper) in 1940 when the basal cover of blue grama was only 13 percent. This increased in a single year (lower) to 21.6 percent.

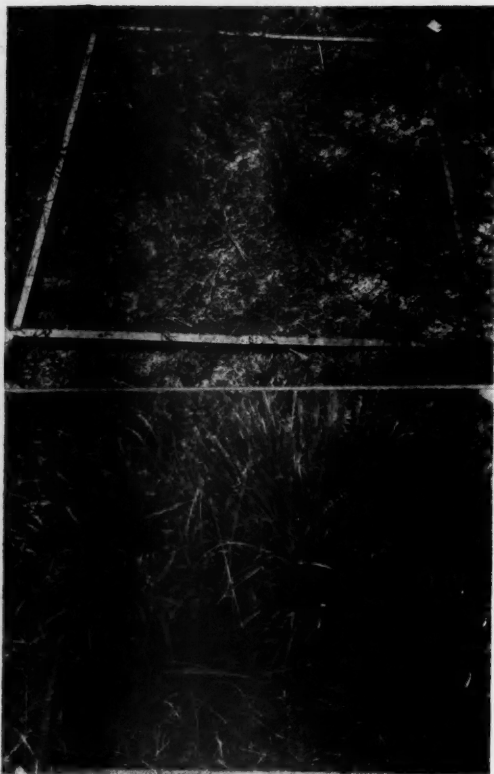


FIG. 16. Quadrat 7 of side-oats grama: (upper) in 1940, with a basal cover of only 2.5 percent; (lower) in 1942 after two years very favorable for growth. Basal cover is about 14 percent.

TABLE 2. Average basal area of the several species of grasses during each autumn, 1940 to 1944, as measured by the pantograph-chart quadrat.

Species	1940	1941	1942	1943	1944
BLUE GRAMA AND BUFFALO GRASS					
<i>Bouteloua gracilis</i> .....	8.8	16.5	20.9	21.8	25.2
<i>Buchloe dactyloides</i> .....	4.0	18.9	25.9	37.8	45.5
<i>Sporobolus cryptandrus</i> .....	0.0	0.2	1.1	1.0	0.4
<i>Bouteloua curtipendula</i> .....	0.0	0.0	0.2	0.3	0.4
BLUE GRAMA					
<i>Bouteloua gracilis</i> .....	8.8	15.5	16.5	13.0	15.1
<i>Bouteloua curtipendula</i> .....	0.0	0.8	0.9	1.5	1.7
SIDE-OATS GRAMA					
<i>Bouteloua curtipendula</i> .....	1.7	9.3	14.9	19.7	31.5
<i>Sporobolus cryptandrus</i> .....	0.0	1.1	1.6	0.6	0.1
MIXED GRASSES					
<i>Bouteloua gracilis</i> .....	3.7	8.0	6.6	6.9	7.8
<i>Buchloe dactyloides</i> .....	1.2	13.5	24.1	24.5	34.6
<i>Bouteloua curtipendula</i> .....	0.8	4.4	5.1	7.3	13.5
<i>Sporobolus cryptandrus</i> .....	0.0	3.2	4.0	5.5	3.5

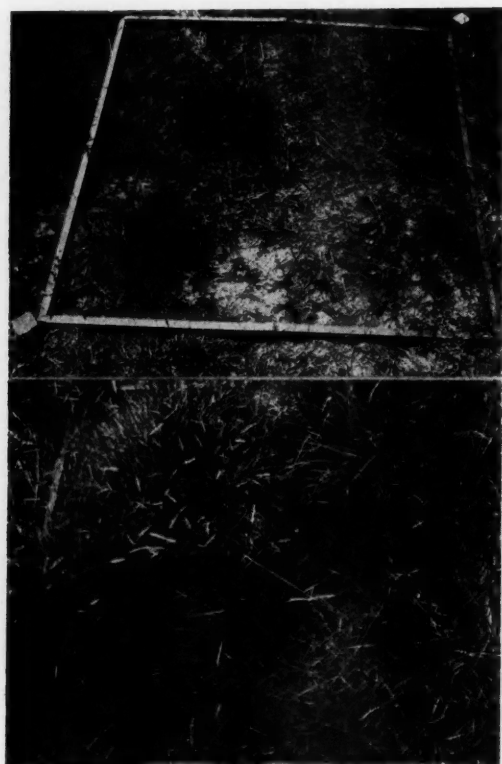


FIG. 17. Quadrat 2 of blue grama and side-oats grama. From a basal cover of 5.8 percent in 1940 (upper) it increased to 22.5 in 1942 (lower), and was 36 percent in 1944.

TABLE 3. Total basal area of perennial grasses in each of 20 quadrats each year and average basal cover in each type of quadrat.

Quadrat	1940	1941	1942	1943	1944
BLUE GRAMA AND BUFFALO GRASS					
1.....	14.7	48.1	61.4	95.3	94.6
3.....	12.5	34.4	44.7	50.5	64.2
5.....	14.2	28.0	46.6	58.5	63.4
6.....	9.5	39.1	76.0	87.0	94.2
8.....	5.2	45.8	54.0	71.5	86.1
9.....	19.5	46.7	47.5	87.8	95.5
10.....	14.9	34.0	45.9	46.0	86.8
11.....	14.7	32.5	40.0	45.2	35.7
16.....	8.4	19.8	32.2	38.7	52.0
18.....	5.1	32.3	39.9	42.2	58.7
20.....	22.3	32.6	42.9	45.9	55.9
Average.....	12.8	35.8	48.3	60.8	71.6
BLUE GRAMA					
4.....	4.5	10.9	11.7	13.6	6.5
14.....	13.0	21.6	23.9	17.0	27.0
Average.....	8.8	16.3	17.8	15.3	16.8
SIDE-OATS GRAMA					
7.....	2.5	8.8	14.1	20.7	29.7
12.....	1.4	10.8	14.9	13.3	38.7
13.....	1.2	16.6	25.2	31.3	41.4
17.....	0.7	11.0	21.2	41.5	51.1
19.....	2.7	9.5	15.8	2.4	4.2
Average.....	1.7	11.3	18.2	21.8	33.0
MIXED GRASSES					
2.....	5.8	21.5	22.5	31.3	35.9
15.....	5.5	36.6	57.0	56.8	82.8
Average.....	5.7	29.1	39.8	44.1	59.4

and fairly rapidly from 1.7 to 33.0 percent cover. In the quadrats of mixed grasses, the basal area increased regularly to about ten times the cover in 1940.

The changes in plant yield from the drought years of 1939 and 1940 to the very wet one in 1941 are given in Table 4.

Increase in production of short grasses and mid grasses in one year was nearly ten-fold. Dry weight of forbs increased four-fold and weeds in about the same amount.

A study of the manner and rate of change in the composition of vegetation after the soil is once occupied by perennial grasses has been found to be very slow. The writers are therefore led to believe that if this prairie had not been broken but remained

TABLE 4. Grams of vegetation produced each of several years in 20 meter quadrats in the prairie at Phillipsburg, 1939 to 1941.

Year	Short grass	Mid grass	Forbs	Weeds	Total
1939.....	682	844	...	2,152	3,678
1940.....	272	32	139	1,965	2,408
1941.....	2,113	329	571	7,572	10,585



ungrazed, probably many years would have been required for the reduction of the short grasses to their former abundance in a normal mixed prairie cover.

### SUMMARY

The history of a typical area of mixed prairie near Phillipsburg in north-central Kansas is recorded. Selected in 1920 as representative of the less xeric type of mixed prairie, drought and dust had reduced it over much of its area to a disclimax of buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) before it was broken in 1945.

The nature of the original vegetation, the degree to which it was damaged by early severe drought, and its vicissitudes during the seven years of drought were studied by one or two examinations yearly. These examinations were supplemented near the end of the drought by annual measurements of basal area in 20 widely distributed meter quadrats.

The fertile, mellow, very fine sandy-loam loess soil absorbs water readily and has a high water-holding capacity. But even during years with normal precipitation, the vegetation was often subjected to moderate soil drought and during later years soil water was often not available at any depth to 5 feet for many days.

The mid grasses, little bluestem (*Andropogon scoparius*), side-oats grama (*Bouteloua curtipendula*), and western wheat grass (*Agropyron smithii*), together with taller ones—big bluestem (*Andropogon furcatus*), Indian grass (*Sorghastrum nutans*), and nodding wild rye (*Elymus canadensis*)—alternated with blue grama and buffalo grass or formed an open layer above them. About 50 species of forbs, many of which formed extensive societies, were found.

Great damage was done by a single year of drought and dust burial in 1933. All plants suffered heavy losses; there was no living little bluestem and about half of the big bluestem had died. The understory of several low-growing grasses and forbs had completely disappeared. Although blue grama and buffalo grass had lost heavily, they alone recovered rapidly with spring rains. Only about 15 of the species of forbs remained; most of these were very deeply rooted or possessed other underground storage organs. The spring rains had promoted the development of a host of annual weeds, which occurred throughout but especially where a layer of dust 2.5 inches or more in thickness had destroyed practically all of the native vegetation.

Intense drought alternating with periods of rainfall sufficient to revive the vegetation or even promote vigorous growth characterized a period of 5

years. The net result was a gradual decrease in tall and most mid grasses and less xeric forbs, offset by an increase in short grasses and side-oats grama. A population of annual weeds, although often greatly dwarfed, was characteristic.

A period of extreme drought, including the summer and fall of 1939 and the year 1940, followed. In the spring of 1940 only a little vegetation of any kind was left alive. Chief perennials were buffalo grass and blue grama. In fact, seedlings and new tufts were so plentiful that it seemed that short grasses might dominate the whole prairie. Conversely, nearly all of the mid and tall grasses had died or were dormant. Side-oats grama had apparently suffered a total loss. Native forbs were reduced to remnants of 11 species.

Heavy rainfall, beginning in 1941, followed the dry years. Conditions were very favorable to growth, but except for the short grasses there was little native vegetation to profit from the changed environment, and the supply of seed was at a low ebb. Moreover, development of short grasses was hindered by a rank growth of little barley (*Hordeum pusillum*) which grew tall and thickly. By midsummer the prairie had the aspect of a short grass disclimax, except for alternates consisting of about 20 annual weeds, and, in places, revived side-oats grama. Other perennial grasses were few.

The year 1942 marked the continued spreading of the short grasses, and the consolidation of a formerly open cover. An average gain from 13 percent (1940) to 48 percent was recorded in 11 meter quadrats and much greater gains were common. The average basal cover was about 50 percent and the foliage cover was 80 to 100. Blue grama still slightly exceeded buffalo grass in abundance. This carpet of short grass was 6 to 8 inches thick. The scattered relict stands of side-oats grama were being heavily invaded by buffalo grass which threatened to replace them.

During the next two years buffalo grass especially spread very rapidly and greatly exceeded blue grama in amount. Quadrats gave an average basal cover of more than 70 percent of short grasses. Usually they were so tall and dense that the soil was completely concealed. But elsewhere there were interspaces where annual weeds, mostly horseweed (*Lepidion canadense*), grew to 3 or 4 feet in height. Little barley and most low-growing weeds had nearly disappeared. Mid and tall grasses were nowhere abundant, although remnants of many could be found.

Thus, drought and dust unaided by grazing had reduced a sample area of mixed prairie centuries old to a disclimax of short grasses. Breaking the sod in 1945 ended the study abruptly.



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